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Many Paths to a Common Destination: Morphological Differentiation of a Functionally Convergent Visual Signal

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ABSTRACT: Understanding the interacting outcomes of selection and historical contingency in shaping adaptive evolution remains a challenge in evolutionary biology. While selection can produce convergent outcomes when species occupy similar environments, the unique history of each species can also influence evolutionary trajectories and result in different phenotypic end points. The question is to what extent historical contingency places species on different adaptive pathways and, in turn, the extent to which we can predict evolutionary outcomes. Among lizards there are several distantly related genera that have independently evolved an elaborate extendible dewlap for territorial communication. We conducted a detailed morphological study and employed new phylogenetic comparative methods to investigate the evolution of the underlying hyoid that powers the extension of the dewlap. This analysis showed that there appear to have been multiple phenotypic pathways for evolving a functionally convergent dewlap. The biomechanical complexity that underlies this morphological structure implies that adaptation should have been constrained to a narrow phenotypic pathway. However, multiple adaptive solutions have been possible in apparent response to a common selection pressure. Thus, the phenotypic outcome that subsequently evolved in different genera seems to have been contingent on the history of the group in question. This blurs the distinction between convergent and historically contingent adaptation and suggests that adaptive phenotypic diversity can evolve without the need for divergent natural selection.

Keywords: adaptation, agamidae, convergence, iguanidae, phylogenetic, phylogenetic principal component analysis.

Introduction

Parallel and classical convergent evolution is the repeated evolution of similar phenotypes through common or different genetic processes, respectively (Conte et al. 2012; Ord and Summers 2015). This phenomenon offers unique opportunities to study selective determinism and the predictability of adaptive evolution (Eroukhmanhoff et al. 2009). Selection can produce relatively predictable outcomes when species occupy similar habitats (Langerhans et al. 2006), but the unique history of each species is also likely to influence its evolutionary trajectory (Huey et al. 2000; Langerhans and DeWitt 2004). Determining the relative role of selection and historical contingency in adaptive evolution remains a major challenge in evolutionary biology. It also has important implications for our general understanding of the adaptive process.

For example, the extent that historical contingency places species on different adaptive trajectories has clear ramifications for the extent to which we can predict evolutionary outcomes and when we can expect adaptive convergence to occur among taxa (Gould 1989; Taylor and McPhail 2000; Lenormand et al. 2009; Spor et al. 2014; Ord and Summers 2015). At a basic level, adaptive convergence is expected to become increasingly less likely among taxa as the length of evolutionary time separating taxa increases (Ord and Summers 2015). This is because the longer taxa evolve independently from one another, the greater stochastic factors in the evolution process (e.g., random mutation, genetic drift) and differences in past selection regimes will culminate in divergent present-day phenotypes among taxa. Yet there are many textbook examples of convergent adaptations among distantly related taxa, such as the evolution of the wing in dinosaurs, birds, and mammals from adaptive changes in forelimb morphology (Campbell and Reece 2002). Nevertheless, in many of these examples, the specific phenotypic changes that underlie convergences in function can be quite different; for example, different aspects of the forelimb have been modified in different ways to produce a wing for the same adaptive outcome of powered flight. That is, historical contingency likely plays some role in shaping all adaptation, convergent or otherwise.

Conversely, adaptive diversity among taxa is generally expected to occur following divergences in selection regimes among taxa, but recent studies have suggested that the con-

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tingent nature of the evolution process can in itself produce adaptive diversity despite taxa being exposed to virtually the same selection pressure (e.g., McGee and Wainwright 2013). Many populations of North Pacific threespine stickleback fish exhibit different mouth structures but still have similar suction capacity in apparent response to the common selection pressure of needing enhanced feeding performance for certain types of prey (McGee and Wainwright 2013). That is, these fish have converged on a similar functional (adaptive) outcome through different phenotypic pathways. Similarly, isolated populations of North American shrews show ecological convergence in the form of similar diets despite distinct mandibular morphologies (Young et al. 2010). Each of these examples likely reflects contingent factors of each taxon's unique evolutionary history making some morphological changes more likely than others in response to selection pressures that appear very similar among those taxa. These studies also tend to refute the argument that the impact of past history on adaptation can constrain lineages to a suboptimal adaptive outcome because it limits the extent to which organisms can respond to selection (e.g., Gould 1989). This rests on the notion of a single "best" adaptive solution for any given selection environment.

In this study, we used a well-known example of a convergent trait employed in the same functional capacity in distantly related lineages of lizard—a large extendible throat fan called a dewlap that is used by adult males for conspicuous territorial communication—and new phylogenetic comparative methods that enable the objective classification of the underlying morphology of a trait into distinct or common morphotypes. The dewlap is a defining characteristic of Caribbean *Anolis* lizards and putatively conveys species identity cues through its color and pattern that allow congeners to coexist in large sympatric communities (Streelman and Danley 2003; Losos 2009; Macedonia et al. 2013). However, empirical research has shown that the dewlap is likely to be especially important for territorial males in enhancing the detection of associated head bob displays by distant-territory neighbors (Ord and Stamps 2008) and might in itself provide additional cues on potential fighting ability given that its size is correlated with bite performance in some species (Vanhooydonck et al. 2005). Remarkably similar dewlaps also exist in several other distantly related lizard groups (e.g., *Draco*, *Sitana*, and *Otocryptis*; Mori and Hikida 1994; Bahir and Silva 2005; Ord et al. 2015). Additionally, other lizards exhibit large hanging throat appendages that are often conspicuously colored, while still others present brightly colored throat patches and/or inflatable or partly extendible throat sacks as part of territorial displays (reviewed in Ord et al. 2015). The selective pressure driving the evolution of these conspicuous throat structures also seems to be a need for improving the signal efficiency of territorial displays: species that possess an extendible dewlap or some other conspicuously colored hanging throat appendage are predominantly found in forest habitats, where visual communication is more difficult because of low ambient light conditions and increased "visual noise" from dense and windblown vegetation (Ord et al. 2015; see also Stuart-Fox and Ord 2004).

The outward appearance of the dewlap on extension is strikingly similar in some genera, such as the typical disk-shaped dewlap of *Anolis*, *Sitana*, and *Otocryptis* (Losos 2009), whereas other genera such as *Draco* have more angular dewlaps and additional elaborations in the form of laterally extensible neck flanges (McGuire and Dudley 2011). These similarities and differences in the appearance of the dewlap (e.g., see fig. 1*A*) suggest that the hyoid apparatus (fig. 1*B*), which is the underlying structure that powers the dewlap extension (Ord et al. 2013*b*), may have evolved through both similar (i.e., convergent) and different (i.e., divergent) morphological trajectories. This in turn implies potential differences in the extent to which the signature of past history has been retained in present-day phenotypes—the morphology of the dewlap—despite a broadly consistent and extensive time frame of separation among taxa (more than 100 million years; Pyron and Burbrink 2014). To resolve this, we investigated the evolution of the hyoid across two lizard families, the iguanids and the agamids. First, we examined the evolutionary relationships among the components of the hyoid to identify orthogonal axes of morphological variation. Second, we applied a recently developed phylogenetic comparative method to objectively identify distinct and convergent hyoid morphotypes based on these orthogonal morphological axes and to reconstruct the evolutionary history and adaptive landscape of the hyoid as it relates to the evolution of the dewlap and other conspicuous throat structures (e.g., the evolution of large hanging appendages or partially extendible color badges). Finally, we examined the rate of evolution of the hyoid apparatus and the extent to which the evolutionary dynamics of morphologies that generate a large moving dewlap differ among lineages with a dewlap and other lineages that exhibit different types of throat ornamentation or lack ornamentation altogether. Our objective was to identify the range of ways that the same adaptive trait can evolve in evolutionary-disparate lineages, specifically the repeated evolution of a dewlap for territorial communication in taxa that share little in their evolutionary history with one another.

Material and Methods

Data Collection

The goal of our study was to identify structural similarities and differences in hyoid morphology across evolutionary-

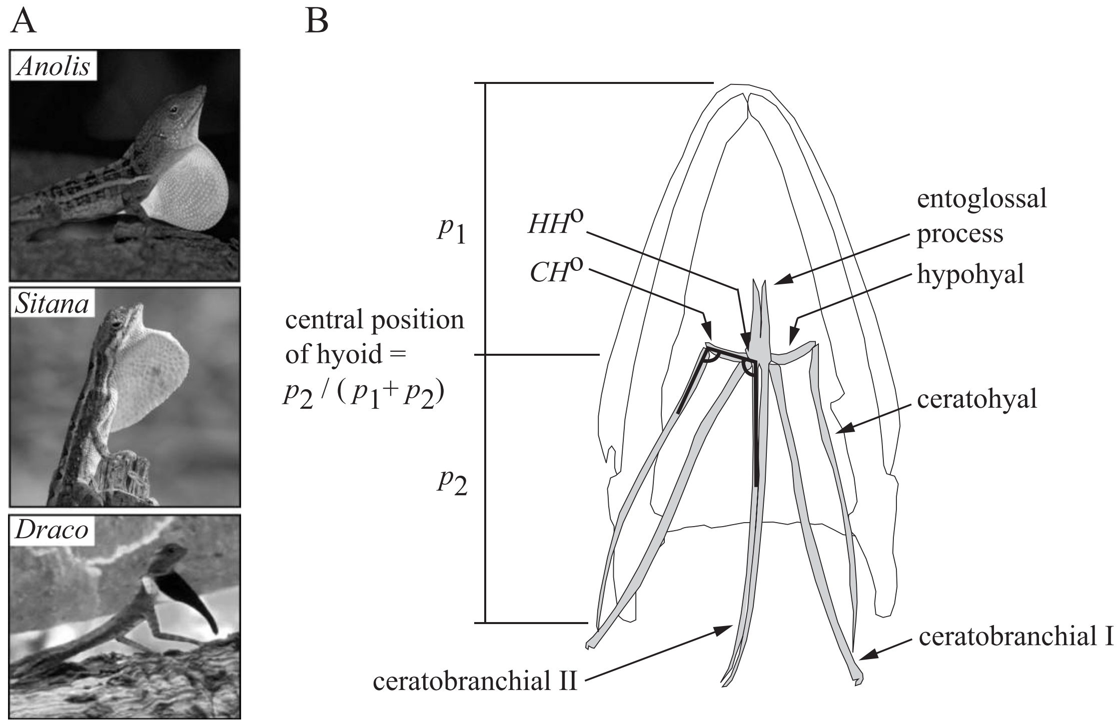


Figure 1: Throat morphology of iguanid and agamid lizards. *A*, Example dewlaps as found in the Jamaican iguanid *Anolis lineatopus* (photo credit: Jonathan Losos), Indian agamid *Sitana ponticeriana* (photo credit: Ambika Kamath), and Malaysian agamid *Draco melanopogon* (photo credit: Terry Ord). *B*, Measures taken of the hyoid. The central position of the hyoid was measured as the distance of the point where the hypohyal joins the second ceratobranchials to the end of the lower jaw (p_2) divided by the total length of the lower jaw (p_1+p_2).

disparate taxa. To this end, we measured characteristics of the hyoid apparatus in adult male specimens of 57 species representing 29 genera across the Agamidae (37 species) and the extended family of the Iguanidae (21 species). This survey included a range of closely related dewlapped and nondewlapped taxa, and although not exhaustive in total species coverage of both families, it was comprehensive in including representatives of most of the diversity in throat ornamentation exhibited by both families (e.g., moveable dewlaps, static throat appendages, no morphological modifications to the throat; reviewed in Ord et al. 2015). Morphological measurements of nine *Anolis* species ($n = 14$ specimens) were obtained from photographs of specimens that were cleared and stained with alizarin red and alcian blue by a previous study (Ord et al. 2013*a*; NB: the study of small-scale evolutionary changes in the hyoid among species of the same genus was not a key objective of this study [instead see Ord et al. 2013*a*], and these *Anolis* species were included to provide a general benchmark of the level of variation that can occur among closely related taxa exhibiting the same type of throat ornament, i.e., a moveable dewlap). For the remaining species, measurements were taken from CT scans of museum specimens.

We used the ImageJ software (Schneider et al. 2012) to measure the length and the midway width of the five major components that make up the left side of the hyoid apparatus: the entoglossal process, hypohyal, ceratohyal, first ceratobranchial, and second ceratobranchial (fig. 1*B*; see also appendix for a more detailed description of the different morphological structures and why they are important). We also measured the angles between the hypohyal and the ceratohyal (CH°) and between the hypohyal and the second ceratobranchials (HH°). These angles have been implicated as influential in the articulation of the hyoid during dewlap extension in *Anolis* (Ord et al. 2013*a*). The central position of the hyoid was calculated as the distance from the point where the hypohyal joins the second ceratobranchial to the end of the lower jaw divided by the total length of the lower jaw (fig. 1*B*). This measurement was taken because preliminary inspection of specimens suggested that the position of the hyoid had the potential to vary widely among species. Finally, snout-to-vent length (SVL) was taken from whole specimens prior to processing as a measure of body size.

For 17 species, we were able to obtain two to five specimens for each species (median = 2). To assess the extent to which the hyoid might vary among adult males within species, we computed the coefficient of variation with a correction for sample size (CV*; Zar 1999) across specimens for each species and compared these estimates to the CV* computed across the means of all 57 species for the same characteristic. In all cases, across-species variance was substantially higher than the variance estimated among specimens of the same species (CV* across species was between two and five times greater than within species). We therefore assumed that within-species variation would have a negligible impact on patterns documented among species (see Harmon and Losos 2005). Data from multiple specimens were averaged to provide a single estimate for each species.

Size-free residuals were obtained for length and width data of hyoid components based on a phylogenetic regression of the natural log of each hyoid measure on the natural log of SVL. This regression used a phylogenetic generalized least squares (PGLS) regression model implemented in the R package "ape," version 3.1-4 (Paradis et al. 2004), using Pagel's λ statistic (Pagel 1999) and excluded the dewlapped genera *Anolis*, *Draco*, *Otocryptis*, and *Sitana*. These exclusions were made because initial analyses showed that species possessing a moveable dewlap were often prominent outliers, so much so that including them resulted in nonsensical regression estimates—regressions of such poor fit to be uninformative—and subsequently produced extensive variance in residuals that was unlikely to be biologically relevant (NB: this problem was also an issue for including body size directly in principal component analyses; see below). To avoid this, PGLS regressions were initially parameterized without dewlapped genera but then used to compute residuals for all species (dewlapped and nondewlapped) in a separate calculation. Visual inspection of plots of size-free residuals calculated in this way confirmed that this approach provided a more realistic view of the size of hyoid components relative to species body size. The data used in analyses are deposited in the Dryad Digital Repository: http://dx.doi.org/10.5061/dryad.61f72 (Hagman and Ord 2016).

Phylogenetic Comparative Analyses

The main comparative analyses of hyoid evolution were conducted in three parts. First, we applied a phylogenetic principal component analysis (pPCA; Revell 2009) using the R package "phytools," version 0.3-93 (Revell 2012), and the option λ to identify evolutionarily orthogonal axes of morphological variation. Because the ceratohyals were either absent or undetectable in CT scans of the dewlapped agamid *Sitana ponticeriana*, we ran the pPCA with and without the species. In both analyses, two general axes of variation were identified that corresponded to the HH° (the angle between the hypohyals and the second ceratobranchials) and the relative lengths of the hypohyals and the second ceratobranchials, respectively. These same characteristics have been previously identified as functionally important in powering the extension of the dewlap in *Anolis* (Ord et al. 2013*a*). We therefore used the first two principal components (pPC) associated with these characteristics from the pPCA that included *S. ponticeriana* to test for similarities and differences in the hyoid among species.

Second, we applied the R package "SURFACE," version 0.4-1 (Ingram and Mahler 2013), to these first two principal components to identify separate and potentially convergent hyoid morphotypes. SURFACE applies the Hansen model of stabilizing selection (Hansen 1997) and a stepwise Akaike information criterion procedure to identify separate adaptive regimes across the phylogeny based on multivariate phenotypic data that are assumed to be evolutionarily orthogonal. The analysis also identifies the number of instances where phenotypes have converged independently on the same adaptive regime in different parts of the phylogeny. To benchmark these analyses, we compared results to null distributions of the number of regimes (i.e., the number of separate hyoid morphotypes) and the number of convergences in those regimes that would be expected by chance under a Brownian motion model of evolution (e.g., see Stayton 2008). These null distributions were generated from 1,000 simulations of phenotypic data along the phylogeny. To assess the general sensitivity of our findings to the specific data entered into the analysis, we also repeated analyses with additional principal components (up to four), principal components generated from pPCAs without *S. ponticeriana*, and raw data for individual hyoid components found to load prominently on different PC axes (e.g., HH° and the length of the second ceratobranchials). Results were similar across all of these analyses, and we subsequently focused on those results obtained from the analysis of the first two principal components from the pPCA inclusive of the dewlapped species *S. ponticeriana*.

Finally, we investigated possible changes in the rate of evolution for each hyoid component across the phylogeny using the R package "geiger," version 2.0.3 (Harmon et al. 2008), and the function "rjmcmc.bm" with a relaxed-rates Brownian motion model (Eastman et al. 2011). The proposal width for Markov sampling was assessed for each hyoid component separately using "calibrate.rjmcmc" and 10,000 proposal steps. We then ran three independent chains for 20,000,000 generations with a sampling interval of 3,000 generations. These runs were then combined, with the first 50% of generations excluded as burn-in. Diagnostics were run using the R package "coda," version 0.16-4 (Plummer et al. 2006), to confirm adequate chain mixing.

The phylogeny used in all analyses was the time-calibrated tree of squamate reptiles developed by Pyron and Burbrink (2014) and pruned down to the species of interest using Mesquite, version 3.01 (Maddison and Maddison 2010). We first checked and updated species synonyms using the Reptile Database (http://www.reptile-database.org; Uetz and Hošek 2013).

Five species were not represented in the tree and were positioned in the following ways: *Acanthosaura nataliae* was positioned as *Acanthosaura capra*, which was present in the Pyron and Burbrink (2014) phylogeny, because both species extensively overlapped in their distribution and were the only ones to do so in the genus; *Hypsilurus godeffroyi* was positioned within the New Guinea clade based on its distribution and given the median branch length of species in that clade; *Japalura swinhorniis* was positioned with the other Taiwanese *Japalura* and given the median branch length of other geographically adjacent species in the genus; *Otocryptis beddommii* was positioned as the sister taxa of *Otocryptis wiegmanni*, with a branch length arbitrarily set as the median branch length of species in the sister group of *Acanthosaura*; and *Polychrus liogaster* was arbitrarily positioned as the sister species to *Polychrus marmoratus* with the median branch length of other species in that genus. All analyses were replicated using phylogenies that did and did not include these five species, and findings were broadly consistent. Instances where differences in results were relevant for the interpretation of findings are discussed.

Results

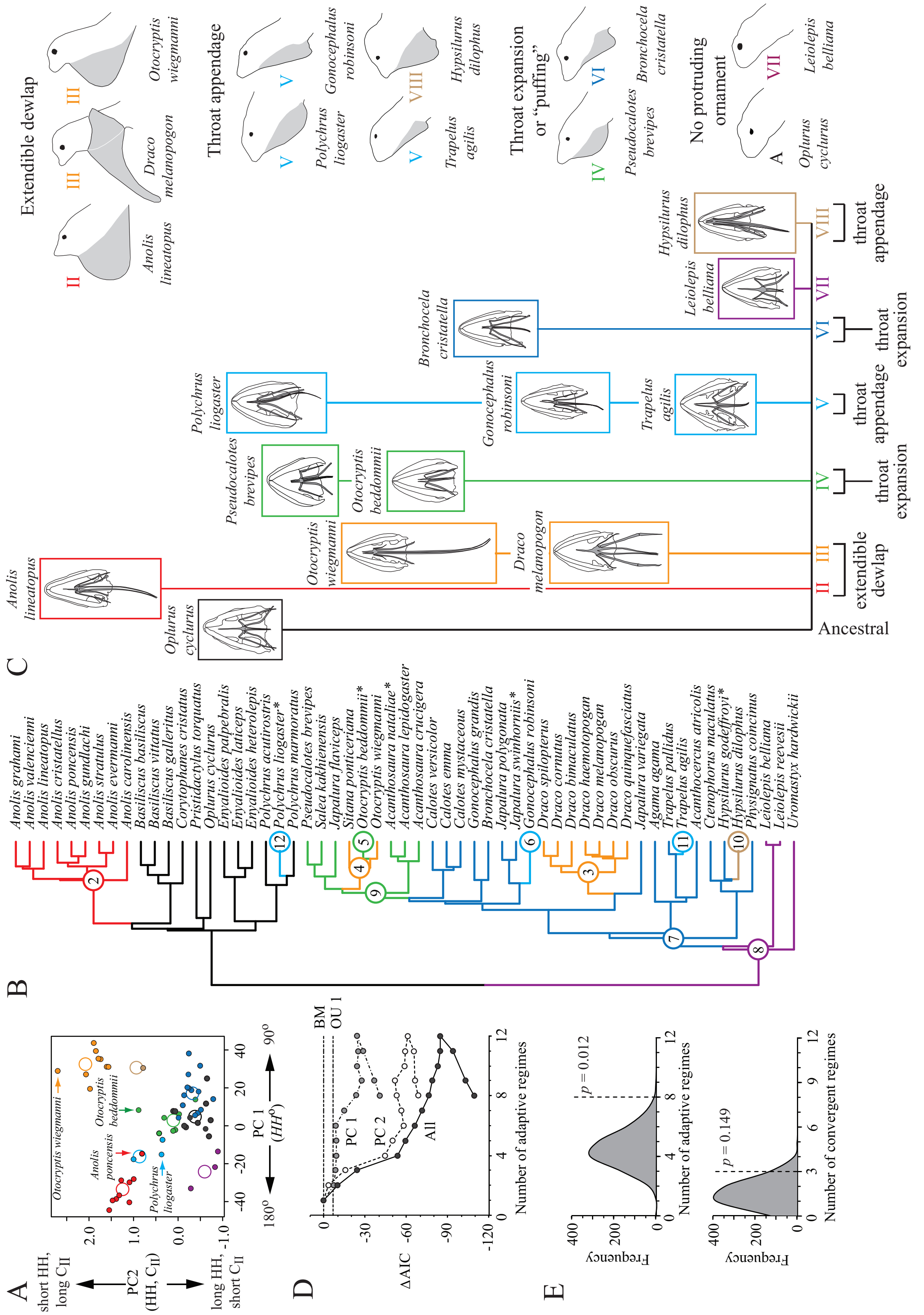
Orthogonal Axes of Hyoid Variation

Results from pPCA with and without *Sitana ponticeriana* were consistent in showing pPC1 explaining most of the

Table 1: Phylogenetic principal component analysis (pPCA) of hyoid morphology in iguanid and agamid lizards

	pPC1	pPC2	pPC3	pPC4	pPC5
a. All traits, without *Sitana* ($N_{\text{species}} = 56$):					
Entoglossal process, length	−.22	−.09	−.46	−.25	−.27
Entoglossal process, width	.23	.03	**−.51**	−.28	**.62**
Hypohyal, length	−.26	.07	**−.89**	.12	−.21
Hypohyal, width	.05	−.09	−.37	**−.52**	**.53**
Ceratohyal, length	−.07	−.22	−.40	**−.58**	−.39
Ceratohyal, width	.11	−.29	**−.66**	**−.50**	−.08
Ceratobranchial I, length	.26	−.27	.18	**−.60**	−.22
Ceratobranchial I, width	.27	−.24	−.19	**−.64**	.17
Ceratobranchial II, length	−.01	−.25	**.68**	**−.55**	−.33
Ceratobranchial II, width	.09	−.32	.18	**−.66**	.23
HH°	**−.94**	−.33	.00	.00	.00
CH°	**.97**	−.25	.00	.00	.00
Central position of hyoid	.33	−.07	.23	**−.58**	−.07
Standard deviation	2.199	.662	.073	.050	.036
% variation	.915	.083	.001	.000	.000
Cumulative % variation	.915	.998	.999	.999	.999
λ	.52				
b. Subset of traits, with *Sitana* ($N_{\text{species}} = 57$):					
Entoglossal process, length	−.23	−.33	−.36	**.61**	**.56**
Entoglossal process, width	.23	−.34	**−.64**	−.37	.27
Hypohyal, length	−.27	**−.90**	−.09	.19	−.26
Hypohyal, width	−.04	−.17	**−.75**	−.31	.09
Ceratohyal, length	NA	NA	NA	NA	NA
Ceratohyal, width	NA	NA	NA	NA	NA
Ceratobranchial I, length	.18	.39	**−.53**	.24	−.43
Ceratobranchial I, width	.17	.08	**−.71**	−.12	−.34
Ceratobranchial II, length	−.02	**.84**	−.27	.39	−.18
Ceratobranchial II, width	−.06	.37	**−.67**	−.11	−.17
HH°	**−1.00**	.00	.00	.00	.00
CH°	NA	NA	NA	NA	NA
Central position of hyoid	.28	.40	−.44	.06	−.36
Standard deviation	1.592	.072	.048	.036	.032
% variation	.996	.002	.001	.001	.000
Cumulative % variation	.996	.998	.999	.999	.999
λ	.62				

Note: Prominent trait loadings (>0.50) are shown in bold. HH° = angle between the hypohyal and the second ceratobranchials; CH° = angle between the hypohyal and the ceratohyal. NA = not applicable.


A
short HH, long C_{II}
PC2 (HH, C_{II})
long HH, short C_{II}
2.0
1.0
0.0
-1.0
-40
-20
0
20
40
180°
90°
PC 1 (HH^{o})
Otocryptis wiegmanni
Otocryptis beddommii
Anolis poncensis
Polychrus liogaster
D
ΔAIC
0
-30
-60
-90
-120
BM
OU 1
PC 1
PC 2
All
Number of adaptive regimes
0
4
8
12
E
Frequency
400
200
0
p = 0.012
Number of adaptive regimes
0
4
8
12
Frequency
400
200
0
p = 0.149
Number of convergent regimes
0
3
6
9
12
B
Anolis grahami
Anolis valenciennii
Anolis lineatopus
Anolis cristatellus
Anolis poncensis
Anolis gundlachi
Anolis stratulus
Anolis evermanni
Anolis carolinensis
Basiliscus basiliscus
Basiliscus vittatus
Basiliscus galleritus
Corytophanes cristatus
Pristidactylus torquatus
Oplurus cyclurus
Enyalioides palpebralis
Enyalioides laticeps
Enyalioides heteroleplis
Polychrus acutirostris
Polychrus liogaster*
Polychrus marmoratus
Pseudocalotes brevipes
Salea kakhienensis
Japalura flaviceps
Sitana ponticeriana
Otocryptis beddommii*
Otocryptis wiegmanni
Acanthosaura nataliae*
Acanthosaura lepidogaster
Acanthosaura crucigera
Calotes versicolor
Calotes emma
Calotes mystaceous
Gonocephalus grandis
Bronchocela cristatella
Japalura polygonata
Japalura swinhonis*
Gonocephalus robinsoni
Draco spilopterus
Draco cornutus
Draco bimaculatus
Draco haematopogon
Draco melanopogan
Draco obscurus
Draco quinquefasciatus
Japalura variegata
Agama agama
Trapelus pallidus
Trapelus agilis
Acanthocercus atricolis
Ctenophorus maculatus
Hypsilurus godeffroyi*
Hypsilurus dilophus
Physignatus concinus
Leiolepis belliana
Leiolepis reevesii
Uromastyx hardwickii
2
12
5
4
9
6
3
11
10
7
8
C
Anolis lineatopus
Oplurus cyclurus
Otocryptis wiegmanni
Draco melanopogon
Pseudocalotes brevipes
Otocryptis beddommii
Polychrus liogaster
Gonocephalus robinsoni
Trapelus agilis
Bronchocela cristatella
Leiolepis belliana
Hypsilurus dilophus
Ancestral
II
III
IV
V
VI
VII
VIII
extendible dewlap
throat expansion
throat appendage
throat expansion
throat appendage
Extendible dewlap
II
Anolis lineatopus
III
Draco melanopogon
III
Otocryptis wiegmanni
Throat appendage
V
Polychrus liogaster
V
Gonocephalus robinsoni
V
Trapelus agilis
VIII
Hypsilurus dilophus
Throat expansion or "puffing"
IV
Pseudocalotes brevipes
VI
Bronchocela cristatella
No protruding ornament
A
Oplurus cyclurus
VII
Leiolepis belliana

variation among species and being dominated by the angle of orientation of the hypohyal in relation to the ceratohyal (CH°) and the second ceratobranchials (HH°; table 1). A secondary axis was generally associated with differences in the length of the hypohyal (negative loadings) and the second ceratobranchials (positive loadings; table 1). The remaining hyoid components tended to load on pPC3 or pPC4.

Evolution of Distinct Hyoid Morphotypes

Using pPC1 and pPC2 generated from the analysis with *S. ponticeriana*, SURFACE identified eight separate hyoid morphotypes (fig. 2*A*–2*D*). This number of morphotypes was unlikely to have been generated by chance ($P = .012$; fig. 2*E*). That is, at least some of these morphotypes are likely to be the product of a deterministic process (i.e., adaptation). For example, they differentiate species that are known to use a large, colorful moving dewlap in territorial display (*Anolis*, *Sitana*, *Otocryptis*, and *Draco*) and those species that possess a large hanging or partially extendible throat ornament (*Gonocephalus* and *Hypsilurus*). The key components of the hyoid that distinguished morphotypes appeared to be those associated with pPC2 (fig. 2*D*), specifically the relative lengths of the hypohyal and second ceratobranchials (table 1, pt. b). These same morphotypes were almost always identified in other SURFACE analyses using additional pPCs or raw data on individual hyoid components. These additional analyses also continued to highlight the dominating effect of the hypohyal and second ceratobranchials in defining morphotypes, which in the dewlapped species have become greatly reduced and elongated, respectively (e.g., cf. probable ancestral morphotype in fig. 2*C*).

Furthermore, our analyses showed that the dewlapped *Anolis* and the dewlapped agamids *Sitana*, *Otocryptis*, and *Draco* occupy distinct regions of morphospace (fig. 2*A*). There were large differences between the two groups in the relative lengths of the hypohyal and second certobranchials (pPC2) and major differences in the angle of orientation of the hypohyal to the ceratobranchials (HH°; pPC1). Visual inspection of the hyoid apparatus emphasizes the underlying differences in morphology between these two dewlapped groups (fig. 2*C*).

Three of the eight morphotypes appeared to have evolved repeatedly in different taxa, but these convergences were generally unconvincing. First, this number of convergences would generally be expected to occur by chance (i.e., through the process of Brownian motion; $P = .149$; fig. 2*E*). Second, two of the three cases of convergence involved species that were positioned in the phylogeny based on taxonomy and biogeography. When these and other species not included in the original phylogeny were excluded from analyses (those highlighted by asterisks in fig. 2*B*), only one instance of convergence continued to be documented between *S. ponticeriana*–*Otocryptis wiegmanni* and species belonging to the genus *Draco*. Visual inspection of the hyoids of these two clades does show similarities, such as massively reduced hypohyals, greatly reduced ceratohyals, and elongated second ceratobranchials (fig. 2*C*). However, noticeable differences still exist, and the inclusion of additional pPCs tended to separate these two groups into distinct (nonconvergent) morphotypes.

Two species belonging to separate morphotypes were found to sit well away from their estimated adaptive peaks: *Anolis poncensis* and *Otocryptis beddommii* (fig. 2*A*). In both cases, these species effectively lack a dewlap but otherwise belong to genera that are dewlapped. In the case of *A. poncensis*, territorial communication has become almost exclusively focused on an elaborate push-up display (see Ord et al. 2013*b*). In the case of *O. beddommii*, it is unclear how accurate the taxonomy of this species is and whether it is in fact closely related to the dewlapped *O. wiegmanni* (i.e., it was one of the species positioned in the phylogeny based on taxonomy; fig. 2*B*). Species from the genus *Polychrus* have also been suggested to use an *Anolis*-like dewlap in territorial communication (Losos 2009), but direct observation of the dewlap display in these species cannot be verified. Our data found

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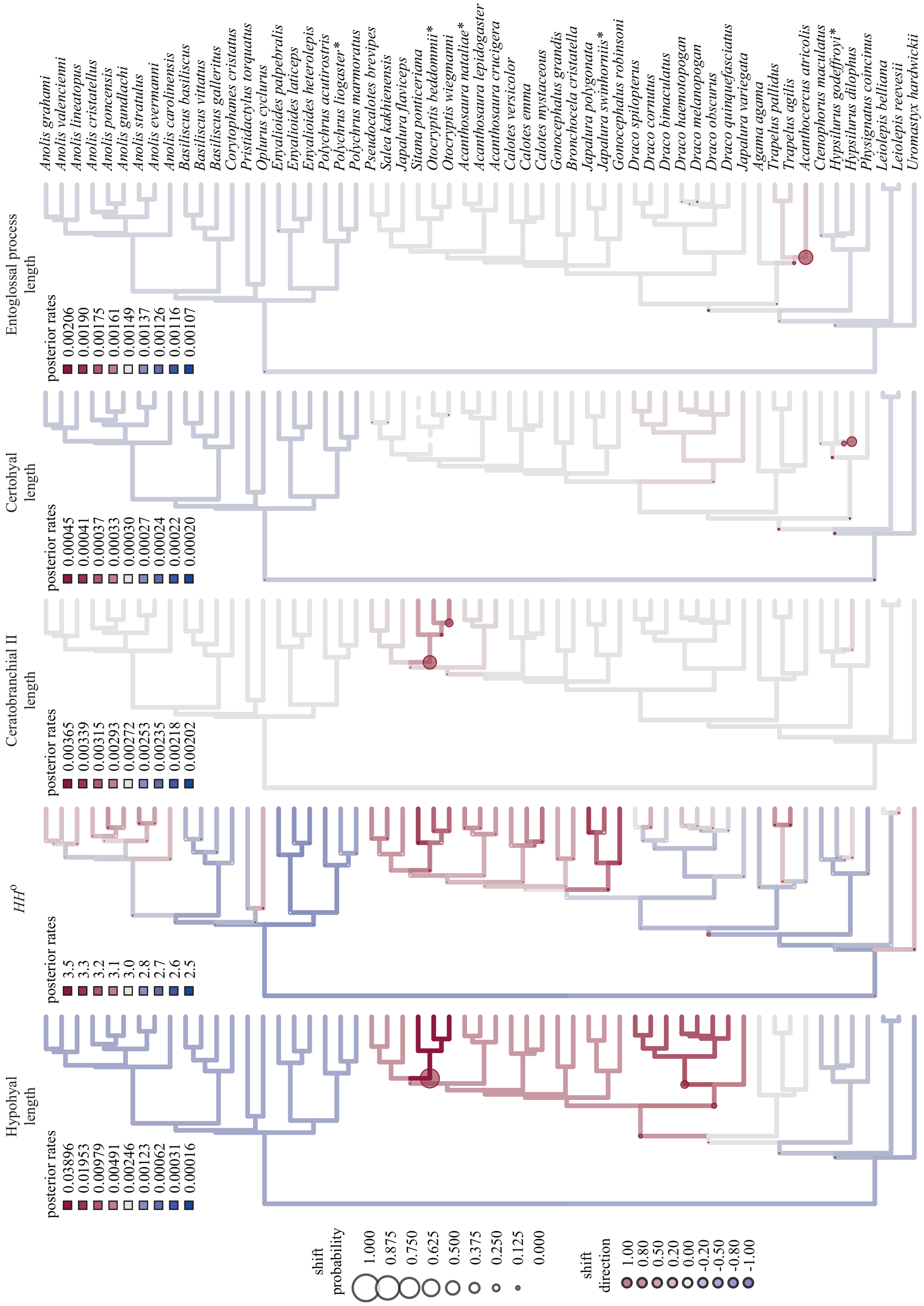
Figure 2: Hyoid morphotypes identified by SURFACE based on the first two phylogenetic principal components (pPCs) in table 1, part b. These pPC axes summarized variation in the hyoid previously identified to be important in powering an extendible dewlap (specifically, the angle between the hypohyal and the second ceratobranchials [HH°] and the relative lengths of the hypohyal and the second ceratobranchial). *A*, The extent to which the hyoid of each species (small filled circles) has converged toward eight unique morphotypes or adaptive peaks (large open circles). *B*, The morphotypes painted onto the phylogeny. Different lineage colors correspond to different hyoid morphotypes, with numbers in circles indicating the order in which each morphotype was identified by the analysis. Asterisks highlight species that were not found in the original phylogeny and were positioned based on taxonomy and biogeography. *C*, Line drawings of representative hyoids for each morphotype and accompanying sketches of the outward appearance of the morphotype in life (roman numerals correspond to hyoid morphotype). *D*, The relative contribution of each of the pPCs in computing the identified morphotypes. Also shown are the computed ΔAICs (difference in the number of Akaike information criterion units from the best-supported model) for a Brownian motion (BM) model that assumes that differentiation in the hyoid has not converged toward any adaptive peak and a single OU (OU 1) model that assumes that the hyoid has evolved toward a single, common adaptive peak. *E*, The null distribution of evolved morphotypes (*top*) and instances of lineages converging independently on the same morphotype (*bottom*) through a nonadaptive BM process. The *P* values correspond to the probability of obtaining by chance the same total number of morphotypes and same number of convergences in morphotypes that were estimated from the empirical data.


Anolis grahami
Anolis valencienni
Anolis lineatopus
Anolis cristatellus
Anolis poncensis
Anolis gundlachi
Anolis stratulus
Anolis evermanni
Anolis carolinensis
Basiliscus basiliscus
Basiliscus vittatus
Basiliscus galleritus
Corytophanes cristatus
Pristidactylus torquatus
Oplurus cyclurus
Enyalioides palpebralis
Enyalioides laticeps
Enyalioides heterolepis
Polychrus acutirostris
Polychrus liogaster*
Polychrus marmoratus
Pseudocalotes brevipes
Salea kakhienensis
Japalura flaviceps
Sitana ponticeriana
Otocryptis beddommii*
Otocryptis wiegmanni
Acanthosaura nataliae*
Acanthosaura lepidogaster
Acanthosaura crucigera
Calotes versicolor
Calotes emma
Calotes mystaceous
Gonocephalus grandis
Bronchocela cristatella
Japalura polygonata
Japalura swinhonis*
Gonocephalus robinsoni
Draco spilopterus
Draco cornutus
Draco bimaculatus
Draco haemotopogon
Draco melanopogan
Draco obscurus
Draco quinquefasciatus
Japalura variegata
Agama agama
Trapelus pallidus
Trapelus agilis
Acanthocercus atricolis
Ctenophorus maculatus
Hypsilurus godeffroyi*
Hypsilurus dilophus
Physignatus concincus
Leiolepis belliana
Leiolepis reevesii
Uromastyx hardwickii
Entoglossal process length
posterior rates
0.00206
0.00190
0.00175
0.00161
0.00149
0.00137
0.00126
0.00116
0.00107
Certohyal length
posterior rates
0.00045
0.00041
0.00037
0.00033
0.00030
0.00027
0.00024
0.00022
0.00020
Ceratobranchial II length
posterior rates
0.00365
0.00339
0.00315
0.00293
0.00272
0.00253
0.00235
0.00218
0.00202
HH^o
posterior rates
3.5
3.3
3.2
3.1
3.0
2.8
2.7
2.6
2.5
Hypohyal length
posterior rates
0.03896
0.01953
0.00979
0.00491
0.00246
0.00123
0.00062
0.00031
0.00016
shift probability
1.000
0.875
0.750
0.625
0.500
0.375
0.250
0.125
0.000
shift direction
1.00
0.80
0.50
0.20
0.00
-0.20
-0.50
-0.80
-1.00

no evidence of an extendible dewlap in two of the species (*Polychrus acutirostris* and *Polychrus marmoratus*), while the third (*Polychrus liogaster*) has a hyoid morphology that might reflect the use of a partially extendible throat appendage, but this is unlikely to be comparable to the *Anolis* dewlap.

Finally, we also found a singular nonconvergent change away from the ancestral morphotype associated with a significant forward shift of the central position of the hyoid in *Hypsilurus dilophus* (highlighted with brown in fig. 2). We could find no reports of dewlap displays in this species, but we have obtained footage reportedly showing the sister species *Hypsilurus boydii* in which a large adult male appears to rapidly extend a dewlap as part of its territorial display (video recorded by G. Johnston). It is interesting that the configuration of the hyoid in *H. dilophus* is very similar to that of confirmed dewlapped genera, albeit with a much more frontal position (fig. 2*C*). The museum specimens used in this study also possessed what externally appeared to be a large dewlap with some resemblance to that of the green iguana (*Iguana iguana*). Taken together, it is possible that *H. dilophus* may represent yet another lineage that has evolved a hyoid that can extend and retract a large dewlap, although this clearly needs to be verified by more observational data.

Dynamics of Hyoid Evolution

Rates of evolution across the phylogeny were found to vary for only five hyoid components, and these are presented in figure 3. Other analyses using a phylogeny excluding those species positioned by taxonomy and biogeography recovered virtually identical results and are not discussed further.

The most evolutionary dynamic components were the length of the hypohyal and its angle of orientation with the second ceratobranchials (HH°). For these components, there appears to have been a progressive increase in the rate of evolution in the southeastern Asian radiation of agamids and major bursts of change occurring in lineages associated with the dewlapped genera *Sitana*, *Otocryptis*, and *Draco*. Both the length of the hypohyal and HH° are believed to be important in the functional performance of a moving dewlap (Ord et al. 2013*a*; appendix). The length of the second ceratobranchials also plays an important role in the extension of the dewlap as it pushes out the dewlap membrane and ultimately determines the overall size of the dewlap at full extension. However, rates of evolution in the length of the second ceratobranchials have been largely consistent across the phylogeny, with the only exception being major bursts of change in lineages associated with the dewlapped genera *Sitana* and *Otocryptis*. Why these particular lineages would exhibit such different evolutionary dynamics is unclear, but all are now dewlapped genera, and it appears that the evolution of these dewlaps has resulted from drastic and rapid changes in these hyoid components relative to other closely related but nondewlapped lineages.

The *Anolis* genus is also dewlapped, but the only noticeable change in hyoid evolutionary rate in this genus was in the HH°. Moreover, rates of change in the *Anolis* HH° appeared to have been quite variable within the genus, especially within the Puerto Rican radiation (*Anolis cristatellus* to *Anolis evermanni* inclusive). The evolution of the rest of the hyoid in *Anolis* has been unremarkable compared to other iguanid lineages. However, we caution that our anole sample is restricted to two groups of closely related species found on Jamaica and Puerto Rico. Our ability to make inferences about the evolution of the dewlap among other anoles more broadly is subsequently limited (i.e., *Anolis* species not found on these two islands).

Rates of evolution for the length of the ceratohyal and entoglossal process were largely consistent across the phylogeny, with some subtle differences between the iguanids and agamids. The iguanids exhibited slightly slower evolutionary rates in the ceratohyal and entoglossal process, while some agamids seem to have had slightly faster evolutionary rates in the ceratohyal (e.g., *Draco* spp. and *Japalura variegata* and *H. dilophus*) or entoglossal (*Trapelus* spp. and *Acanthocercus atricolis*) process.

Discussion

The results of our study show that the convergent use of a large, conspicuously colored dewlap for visual communication in distantly related territorial lizard genera has evolved through divergent changes in the underlying structural morphologies. Adaptation for the same function—a conspicuous moving dewlap for territorial display—has thus been achieved through different evolutionary pathways: alternative modifications to the underlying hyoid responsible for the movement of the dewlap. This demonstrates that there can be multiple adaptive solutions to the same selection challenge (Alfaro et al. 2004; Wainwright et al. 2005; McGee and Wain-

Figure 3: Rates of evolution of various aspects of the hyoid. All hyoid components were analyzed, but only the five presented here showed any obvious variation in evolutionary rates across the phylogeny. Lineage shading corresponds to the absolute rate of evolutionary change (with units of change specific to each trait). The size and color of circles at nodes indicate the probability of a shift in evolutionary rate occurring and its direction: warm colors correspond to an acceleration of evolutionary change, while cool colors correspond to a deceleration of evolutionary change. Asterisks highlight species that were not found in the original phylogeny and were positioned based on taxonomy and biogeography.

wright 2013). It also shows that the unique histories of distantly related taxa can culminate in adaptive diversity without major divergences in selection regime.

Repeated adaptation is often used as evidence that natural selection can override the influence of past history on the trajectory of phenotypic evolution (Van Valen 1991; Dawkins 1996; Conway Morris 2003; Vermeij 2006). The stochastic nature of the evolution process (random mutation) combined with other chance events and past adaptation will tend to influence the types of phenotypes that might arise in taxa (e.g., Gould 1989; Huey et al. 2000). Adaptive convergence in phenotype among taxa suggests that adaptive outcomes are in some sense predictable: similar selection pressures will tend to produce similar adaptive traits in disparate taxa. However, historical contingency may still be apparent in the evolutionary trajectory of many examples of classical convergence if the underlying phenotype of a convergent trait is scrutinized in close enough detail (e.g., McGee and Wainwright 2013). To return to the example presented in the Introduction, the textbook example of convergent wing evolution in birds, bats, and pterodactyls is clearly functionally convergent (powered flight), but the underlying morphological changes in the forearm that have occurred to create the wing have been quite different in each group (e.g., Campbell and Reece 2002). In some ways, then, the role of contingency in influencing the trajectory of adaptive evolution is dependent on how broadly or specific similarities in phenotype or function are defined among taxa. Although the specific morphological changes underlying the evolution of the wing might differ, it has still evolved from the same appendage in birds, bats, and pterodactyls (the forearm), whereas this is not the case for the evolution of the wing in insects. The conclusion of whether the wing reflects classical convergence or a historically contingent outcome is therefore open to interpretation, at least in the case of vertebrates. Examples of repeated evolution that arise from common genetic pathways are perhaps the strongest cases of natural selection erasing the signature of past history from phenotypes (which also implies that adaptive outcomes are constrained to a limited set of outcomes), but many of these occurrences are often among closely related taxa where the differences among taxa in evolutionary history are low (Ord and Summers 2015).

Furthermore, on one hand, there is the issue of whether similar morphological adaptations arise to solve a common selection problem and, on the other hand, whether the dynamics of the evolution process are the same or different in response to selection. For example, in our study the length of the hypohyals has changed to a lesser or greater degree in all dewlapped genera, but the rate of evolutionary change has been quite different, such that there appear to have been big “bursts” of change in *Draco*, *Otocryptis*, and *Sitana* but slower, more incremental changes in *Anolis* (fig. 3). All dewlapped groups are also typified by a lengthening of the second ceratobranchials, although the rate of that change has been clearly accelerated in *Otocryptis* and *Sitana*, whereas rates of change for *Draco* and *Anolis* are indistinguishable from background rates (fig. 3). That is, not only has the dewlap evolved via alternative morphotypes but also the evolutionary dynamics of hyoid modification has been different. Perhaps shifts in habitat might explain these differences in the evolutionary dynamics of the hyoid. For example, the second ceratobranchials of *Draco* and *Anolis*, which are predominantly arboreal, tropical forest lizards (Ord et al. 2015), show similar rates of evolutionary change, whereas in *Sitana* and *Otocryptis*, which are mainly ground-dwelling species (Manamendra-Arachchi and Liyanage 1994), the same components have changed more rapidly. If selection for a large moveable dewlap operates primarily to improve signal transmission in the local habitat (e.g., Ord and Stamps 2008; Ord et al. 2015), then the accelerated rate of change in the second ceratobranchials of *Sitana* and *Otocryptis* might reflect a rapid response to selection associated with shifting to territorial communication from the ground, where visibility is likely to be quite different than in the trees. While the selection pressure is arguably the same for terrestrial and arboreal taxa—the need of a dewlap for improved signal efficiency—the differences in the evolutionary dynamics of the morphological changes to the hyoid suggest that circumstances have potentially been different between taxa within the same morphotype.

More generally, for any form of adaptive convergence to occur, taxa need to be subject to the same selection pressure, and the likelihood of this will presumably decrease with the phylogenetic separation of taxa (Ord and Summers 2015). Even if taxa are subject to the same selection pressure, the position of where taxa start from in phenotypic space will also be important in determining whether the same adaptation ultimately evolves in those taxa, which can again reflect the length of evolutionary time that separate taxa from a common ancestor (Ord and Summers 2015). For example, past adaptation to other selection pressures can predispose taxa to follow different paths of least resistance (Losos 2011). In this scenario, if there is only one optimal solution, taxa will either fail to adapt appropriately or necessarily converge on the same adaptation. In this study, the same adaptation of an extendable dewlap for conspicuous territorial communication has evolved independently in distantly related taxa, but this convergence has been achieved through different structural changes to the underlying hyoid. There are consequently several different ways to evolve a dewlap. It remains unclear whether these alternative pathways to a moving dewlap are equally efficient in design (are equally optimal). However, preliminary data and extensive field observations on the display behavior of two of the most disparate genera, *Anolis* and *Draco* (fig. 1*A*), suggest that the alternative hyoid forms in these two groups are at least capable of producing a similar range of extension speeds and extensions in a repeated temporal sequence of display (*Anolis*: Ord et al. 2010; *Draco*: T. J. Ord, unpublished data). The dewlap is also clearly used in a similar manner by males in both groups as well (T. J. Ord, personal observation; cf. also Mori and Hikida 1994 and Humraskar 2008 for *Draco* and Ord 2008 for *Anolis*). Therefore, organisms can and do respond in a variety of comparable ways to the same selection pressure (McGee and Wainwright 2013).

How often we might expect adaptation to be free to vary in response to deterministic processes (selection) or constrained to follow specific evolutionary trajectories depends on how frequently the same ecological problem can be overcome in multiple ways. Our analysis shows that even a complex interdependent morphological structure such as the hyoid, which consists of many moving parts (see appendix for additional discussion), can evolve in a diversity of ways to seemingly achieve the same functional result. Beyond the semantics of how structure and function are defined, the fact that this complexity has not limited the ways in which the hyoid can be modified to produce a moving dewlap implies that multiple adaptive solutions to a given selection problem are potentially common in nature for less biomechanically intricate adaptations.

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APPENDIX

Description of Hyoid Morphology and a Discussion on the Articulation and Performance of Its Structures

The anatomy and biomechanics of the dewlap are well studied in *Anolis* (Bels 1990; Font and Rome 1990; Ord et al. 2013*b*). Extension of the *Anolis* dewlap occurs through a muscular contraction between the first ceratobranchials and the ceratohyals, causing the hypohyals to rotate away from the nose of the lizard, which then protracts and depresses the second ceratobranchials (fig. 1*B*) and extends the dewlap (Ord et al. 2013*a*). The hyoid thus operates as a first-order lever. A recent biomechanical model also shows that the speed at which the dewlap can be extended is dependent not only on the lengths of the second ceratobranchials and the hypohyals, and on their respective orientations to output and input movements, but also on the input speed that the muscular contraction generates (Ord et al. 2013*a*). Although our study did not have the capability to assess muscle physiology, there are clearly a number of ways that the hyoid system can be modified to accomplish the same functional outcome (i.e., a rapid dewlap extension for conspicuous social communication).

Nevertheless, the hyoid is a structure in which change in one component might also be assumed to impact the articulation or performance of other components. Furthermore, the hyoid apparatus provides attachment sites for muscles that control tongue flicking and feeding (e.g., Smith 1986; Bels 1990; Bels et al. 1994). Evolutionary change thus might happen more easily in some components than in others, either because of anatomical constraints or because of genetic or developmental correlations. In other words, constraint on design changes can bias the direction of evolutionary trajectories of adaptations. In the case of the hyoid apparatus, the length of the second ceratobranchials might, for example, change more easily than the length of hypohyals (Ord et al. 2013*a*). Yet our results imply that the most dynamic component of the hyoid associated with the evolution of a dewlap has been the hypohyal, specifically its rapid reduction in length and bursts of evolutionary change in its orientation to the second ceratobranchials. This is interesting because the hypohyal articulates with more components in the hyoid than the second ceratobranchials (fig. 1*B*), but this appears not to have constrained its modification during dewlap evolution. In general, structures that seem to be highly specialized or complex such as the cephalopod and vertebrate eye (e.g., Ogura et al. 2004; Yoshida and Ogura 2011) are more intuitively expected to follow the same evolutionary pathways. By this logic, the dewlap should have evolved in the same or very similar way in agamids and iguanids. This has not been the case, which shows that highly interdependent morphological structures made up of lots of working parts can evolve in a diversity of ways to achieve the same functional result.

Our analyses identified the highest amount of variation among lizard species in the angle of the hypohyals relative to the second ceratobranchials and, to a lesser extent, in the relative lengths of the hypohyals and the second ceratobranchials (table 1, pt. b), indicating that these are the main hyoid characteristics that have diverged among morphotypes and also the components critical for the evolution of an extendible, conspicuous dewlap (fig. 1*B*). There was some evidence for convergence in hyoid morphology among distantly related species, such as *Polychrus liogaster*, *Gonocephalus robinsoni*, and *Trapelus agilis* (highlighted with blue in fig. 2). These species lack dewlaps of the large extendable type found in *Anolis* or *Draco*, and it is unclear whether these examples reflect adaptive convergence or chance similarities generated by the process of Brownian motion (or some other nonadaptive process). However, conspicuous throat color in combination with throat inflation behavior is a common form of communication in lizards and more so than the use of a large extendable dewlap (Ord et al. 2015). *Polychrus liogaster*, *G. robinsoni*, and *T. agilis* all have a throat sack whose outward appearance seems to be more of an inflatable type with a brighter coloration than the rest of the body, suggesting at least broad functional convergence for social communication with the dewlap. The hyoid has gross similarities with species exhibiting an extendible dewlap (e.g., reduced hypohyals and elongated second ceratobranchials; fig. 2*A*, 2*C*), but it is generally less elaborate in form. This hyoid morphotype might therefore provide some clues to what the intermediate step might look like in the evolution of an extendable dewlap.

Literature Cited

Alfaro, M. E., D. I. Bolnick, and P. C. Wainwright. 2004. Evolutionary dynamics of complex biomechanical systems: an example using the four-bar mechanism. Evolution 58:495–503.

Bahir, M. M., and A. J. Silva. 2005. *Otocryptis nigristigma*, a new species of agamid lizard from Sri Lanka. Raffles Bulletin of Zoology 12:393–406.

Bels, V. L. 1990. The mechanism of dewlap extension in *Anolis carolinensis* (Reptilia: Iguanidae) with histological analysis of the hyoid apparatus. Journal of Morphology 206:225–244.

Bels, V. L., M. Chardon, and K. V. Kardong. 1994. Biomechanics of the hyolingual system in Squamata. Pages 197–240 *in* P. Vandewalle, ed. Advances in comparative and environmental physiology. Vol. 18. Biomechanics of feeding in vertebrates. Springer, Heidelberg.

Campbell, N. A., and J. B. Reece. 2002. Biology. 6th ed. Cummings, San Francisco.

Conte, G. L., M. E. Arnegard, C. L. Peichel, and D. Schluter. 2012. The probability of genetic parallelism and convergence in natural populations. Proceedings of the Royal Society B: Biological Sciences 279:5039–5047.

Conway Morris, S. 2003. Life's solution. Cambridge University Press, Cambridge.

Dawkins, R. 1996. The blind watchmaker. Norton, New York.

Eastman, J. M., M. E. Alfaro, P. Joyce, A. L. Hipp, and L. J. Harmon. 2011. A novel comparative method for identifying shifts in the rate of character evolution on trees. Evolution 65:3578–3589.

Eroukhmanoff, F., A. Hargeby, N. N. Arnberg, O. Hellgren, S. Bensch, and E. I. Svensson. 2009. Parallelism and historical contingency during rapid ecotype divergence in an isopod. Journal of Evolutionary Biology 22:1098–1110.

Font, E., and L. C. Rome. 1990. Functional morphology of dewlap extension in the lizard *Anolis equestris* (Iguanidae). Journal of Morphology 206:245–258.

Gould, S. J. 1989. Wonderful life: the Burgess shale and the nature of history. Norton, New York.

Hagman, M., and T. J. Ord. 2016. Data from: Many paths to a common destination: morphological differentiation of a functionally convergent visual signal. American Naturalist, Dryad Digital Repository, http://dx.doi.org/10.5061/dryad.61f72.

Hansen, T. F. 1997. Stabilizing selection and the comparative analysis of adaptation. Evolution 51:1341–1351.

Harmon, L. J., and J. B. Losos. 2005. The effect of intraspecfic sample size on type I and type II error rates in comparative studies. Evolution 59:2705–2710.

Harmon, L. J., J. T. Weir, C. D. Brock, R. E. Glor, and W. Challenger. 2008. GEIGER: investigating evolutionary radiations. Bioinformatics 24:129–131.

Huey, R. B., G. W. Gilchrist, M. L. Carlson, D. Berrigan, and L. Serra. 2000. Rapid evolution of a geographic cline in size in an introduced fly. Science 5451:308–309.

Humraskar, D. 2008. Ecology and behaviour of the Western Ghats flying lizard *Draco dussumieri* in Dandeli wildlife sanctuary. MS thesis. Manipal University, Bangalore.

Ingram, T., and D. L. Mahler. 2013. SURFACE: detecting convergent evolution from comparative data by fitting Ornstein-Uhlenbeck models with stepwise AIC. Methods in Ecology and Evolution 4: 416–425.

Langerhans, R. B., and T. J. DeWitt. 2004. Shared and unique features of evolutionary diversification. American Naturalist 164:335–349.

Langerhans, R. B., J. H. Knouft, and J. B. Losos. 2006. Shared and unique features of diversification in greater Antillean *Anolis* ectomorphs. Evolution 60:362–369.

Lenormand, T., D. Roze, and F. Rousset. 2009. Stochasticity in evolution. Trends in Ecology and Evolution 24:157–165.

Losos, J. B. 2009. Lizards in an evolutionary tree: ecology and adaptive radiation of anoles. University of California Press, Berkeley.

———. 2011. Convergence, adaptation, and constraint. Evolution 65: 1827–1840.

Macedonia, J. M., D. L. Clark, R. G. Riley, and D. J. Kemp. 2013. Species recognition of color and motion signals in *Anolis grahami*: evidence from response to lizard robots. Behavioral Ecology 24:846–852.

Maddison, W. P., and D. R. Maddison. 2010. Mesquite: a modular system for evolutionary analysis. Version 3.03. http://mesquiteproject.org.

Manamendra-Arachchi, K., and S. Liyanage. 1994. Conservation and distribution of the agamid lizards of Sri Lanka with illustrations of the extant species. Journal of South Asian Natural History 1:77–96.

McGee, M. D., and P. C. Wainwright. 2013. Convergent evolution as a generator of phenotypic diversity in threespine stickleback. Evolution 67:1204–1208.

McGuire, J. A., and R. Dudley. 2011. The biology of gliding in flying lizards (genus *Draco*) and their fossil and extant analogs. Integrative and Comparative Biology 51:983–990.

Mori, A., and T. Hikida. 1994. Field observations on the social behavior of the flying lizard, *Draco volans sumatranus*, in Borneo. Copeia 1994:124–130.

Ogura, A., K. Ikeo, and T. Gojobori. 2004. Comparative analysis of gene expression for convergent evolution of camera eye between octopus and human. Genome Research 14:1555–1561.

Ord, T. J. 2008. Dawn and dusk "chorus" in visually communicating Jamaican anole lizards. American Naturalist 172:585–592.

Ord, T. J., D. C. Collar, and T. J. Sanger. 2013*a*. The biomechanical basis of evolutionary change in a territorial display. Functional Ecology 27:1186–1200.

Ord, T. J., D. A. Klomp, J. Garcia-Porta, and M. Hagman. 2015. Repeated evolution of exaggerated dewlaps and other throat morphology in lizards. Journal of Evolutionary Biology 28:1948–1964.

Ord, T. J., and J. A. Stamps. 2008. Alert signals enhance animal communication in "noisy" environments. Proceedings of the National Academy of Sciences of the USA 105:18830–18835.

Ord, T. J., J. A. Stamps, and J. B. Losos. 2010. Adaptation and plasticity of animal communication in fluctuating environments. Evolution 64:3134–3148.

———. 2013*b*. Convergent evolution in the territorial communication of a classic adaptive radiation: Caribbean *Anolis* lizards. Animal Behaviour 85:1415–1426.

Ord, T. J., and T. C. Summers. 2015. Repeated evolution and the impact of evolutionary history on adaptation. BMC Evolutionary Biology 15:137.

Pagel, M. 1999. Inferring the historical patterns of biological evolution. Nature 401:877–884.

Paradis, E., J. Claude, and K. Strimmer. 2004. APE: analyses of phylogenetics and evolution in R language. Bioinformatics 20:289–290.

Plummer, M., N. Best, K. Cowles, and K. Vines. 2006. CODA: convergence diagnosis and output analysis for MCMC. R News 6:7–11.

Pyron, R. A., and F. T. Burbrink. 2014. Early origin of viviparity and multiple reversions to oviparity in squamate reptiles. Ecology Letters 17:13–21.

Revell, L. J. 2009. Size-correction and principal components for interspecific comparative studies. Evolution 63:3258–3268.

———. 2012. Phytools: an R package for phylogenetic comparative biology (and other things). Methods in Ecology and Evolution 3: 217–223.

Schneider, C. A., W. S. Rasband, and K. W. Eliceiri. 2012. NIH Image to ImageJ: 25 years of image analysis. Nature Methods 9:671–675.

Smith, K. K. 1986. Morphology and function of the tongue and hyoid apparatus in *Varanus* (Varanidae, Lacertilia). Journal of Morphology 187:261–287.

Spor, A., D. J. Kvitek, T. Nidelet, J. Martin, J. Legrand, A. Bourgais, D. de Vienne, G. Sherlock, and D. Sicard. 2014. Phenotypic and genotypic convergences are influenced by historical contingency and environment in yeast. Evolution 68:772–790.

Stayton, C. T. 2008. Is convergence surprising? an examination of the frequency of convergence in simulated datasets. Journal of Theoretical Biology 252:1–14.

Streelman, J. T., and P. D. Danley. 2003. The stages of vertebrate evolutionary radiation. Trends in Ecology and Evolution 18:126–131.

Stuart-Fox, D., and T. J. Ord. 2004. Sexual selection, natural selection and the evolution of dimorphic coloration and ornamentation in agamid lizards. Proceedings of the Royal Society B: Biological Sciences 271:2249–2255.

Taylor, E. B., and J. D. McPhail. 2000. Historical contingency and ecological determinism interact to prime speciation in sticklebacks, *Gasterosteus*. Proceedings of the Royal Society B: Biological Sciences 267:2375–2384.

Uetz, P., and J. Hošek. 2013. The Reptile Database. http://www.reptile-database.org.

Vanhooydonck, B., A. Y. Herrel, R. Van Damme, and D. J. Irschick. 2005. Does dewlap size predict male bite performance in Jamaican *Anolis* lizards? Functional Ecology 19:38–42.

Van Valen, L. M. 1991. How far does contingency rule? Evolutionary Theory 10:47–52.

Vermeij, G. J. 2006. Historical contingency and the purported uniqueness of evolutionary innovations. Proceedings of the National Academy of Sciences of the USA 103:1804–1809.

Wainwright, P. C., M. E. Alfaro, D. I. Bolnick, and C. D. Hulsey. 2005. Many-to-one mapping of form to function: a general principle in organismal design? Integrative and Comparative Biology 45:256–262.

Yoshida, M., and A. Ogura. 2011. Genetic mechanisms involved in the evolution of the cephalopod camera eye revealed by transcriptomic and developmental studies. BMC Evolutionary Biology 11: 180.

Young, R. L., M. J. Sweeney, and A. V. Badyaev. 2010. Morphological diversity and ecological similarity: versatility of muscular and skeletal morphologies enables ecological convergence in shrews. Functional Ecology 24:556–565.

Zar, J. H. 1999. Biostatistical analysis. Prentice Hall, Upper Saddle River, NJ.

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