

# Title

## Generalists link peaks in the shifting adaptive landscape of Australia's dragon lizards

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Conceptualization, IGB, JSK, NC; sampling, LGT, JS; data collection ESB, JT, IGB; data curation, IGB, ESB; methodology, NC, IGB; analysis IGB, ST; writing - original draft, IGB; writing - reviewing & editing, all authors; funding acquisition, JSK.

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# Abstract

The adaptive landscape is one of biology's most flexible and intuitive general concepts. This multidimensional space enables us to map individuals, populations, and species to an evolutionary topography, teasing apart what distinguishes entities from one another. A common exercise is clustering species into adaptive peaks which highlight regions of explored trait space, often considered trait optima or adaptive zones. Typically this reveals broad regions of unpopulated and suboptimal trait space that must be traversed between peaks, however, these evolutionary pathways remain poorly understood. Here we use new sequence-capture and linear morphological datasets to investigate the evolution of the adaptive landscape in a group of highly visible and charismatic reptiles: Amphibolurinae dragon lizards (Family Agamidae). We generate a well-supported time-calibrated phylogenomic tree from >5,000 nuclear markers for more than 360 specimens across 176 dragon species, including undescribed diversity, and provide new insights into the diversification of a group that includes iconic species like the frilled-neck lizard, thorny devil, and bearded dragon. By investigating the multivariate morphological evolution of dragon lizards we show that the colonization of Australia was followed by rapid morphological expansion. While the ancestral amphibolurine was likely tree-living, the evolution of the morphological landscape was facilitated by a transition to a generalist form and then subsequent transitions to more specialized ecomorphs. These results provide evidence of an evolutionary pathway for adaptive diversification in a continental radiation.

## 22 Introduction

23 The adaptive landscape has become an indispensable tool for considering and  
24 visualizing evolutionary spaces. In adapting Sewall Wright's (1932) genotypic fitness  
25 landscape to a phenotypic space, GG Simpson (1944) provided evolutionary biologists  
26 a shared vocabulary and conceptual bridge between micro- and macroevolution  
27 (Arnold et al. 2001). At local scales (species or populations) landscapes help us to map  
28 form to fitness. However, at broader scales (species, genera, families) landscapes (often  
29 called morphospaces or functional trait spaces) tell us about the density and position  
30 of peaks, and how communities or clades map to phenotypic space. This can be  
31 valuable in determining the cost of moving between phenotypes, or comparing the  
32 morphological limits of different clades. Importantly, phenotypic landscapes are  
33 dynamic and can vary through time in their characteristics (Marshall 2014), dictating  
34 the persistence and evolution of the species which they represent. As a result, we can  
35 use data from those species to infer parameters of, and changes to, the landscape.

36

37 Despite how it is often visualized (2D, 3D), the adaptive landscape was never limited  
38 to only two or three dimensions. Instead, landscapes can be multidimensional and here  
39 the concept intersects with Hutchinson's (1957) idea of the niche hypervolume. In  
40 multidimensional space we can assess the volume and density of individual peaks, probe  
41 the depths of multidimensional valleys, or detect holes in the landscape hypervolume  
42 (Blonder 2016). Higher dimensionality may also provide paths between peaks that  
43 might not be identifiable with fewer dimensions. The complex topography of the  
44 landscape, including holes, dictates viable paths from existing morphologies into new  
45 ones. As such, the ideas of adaptive radiation and ecological opportunity have long  
46 been entwined with Simpson's view of movement across the landscape (Yoder et al.  
47 2010). With advances in computational power, development of more complex  
48 comparative methods, and larger phenotypic datasets, we can begin to unravel  
49 historical changes to the adaptive landscape and evolutionary responses that helped  
50 develop new forms (Harmon et al. 2005). Importantly, we can ask which axes  
51 facilitate/promote movement into new phenotypic space, and if changes to the  
52 landscape are associated with shifts in traits such as ecology, habitat, geographic range,  
53 and opportunity.

54

55 While evolutionary biologists have been visualizing the adaptive landscape and  
56 determining the relative heights of peaks since Simpson, comparatively little empirical  
57 attention has focused on the movement of lineages to populate new peaks and the  
58 evolution of the landscape through time (but see Marshall 2014; Burin et al. 2023).  
59 This is due in part to the necessity of a high dimensional dataset, well-resolved  
60 phylogeny, and an appropriate organismal group. Here we investigate patterns of  
61 adaptive landscape change and the role of ecology and expanding ranges in the  
62 morphological evolution of Australo-Papuan agamid lizards. Amphibolurine agamids  
63 consist of ~130 species with varied and diverse ecologies, habitat preferences, and  
64 highly imbalanced biogeographic richness. The majority of species (~110 spp.) are  
65 endemic to Australia, where their distributions span the continent's driest deserts and  
66 wettest rainforests. Their morphologies reflect these diverse habitats, ranging from  
67 forest dragons cloaked in spines, squat desert pebble mimics, and include iconic species  
68 such as the frilled-neck lizard (*Chlamydosaurus*) and thorny devil (*Moloch*). To match,  
69 they show a range of ecologies from cryptic arboreal species to sand dune burrowers.  
70 Unique ecomorphologies such as these provide an ideal opportunity to study the tempo  
71 and mode of evolution and the processes driving phenotypic change.

72

73 To address the evolution of the amphibolurine adaptive phenotypic landscape, we  
74 started by generating a sequence-capture dataset to reconstruct the phylogenetic  
75 relationships of Australo-Papuan dragon lizards. To investigate morphological  
76 diversity we collected an extensive phenotypic dataset of 19 linear measurements that  
77 summarize broad axes of variation across the head, body, limbs, and tail. We use  
78 phylogenetic comparative methods to assess the tempo and mode of trait evolution  
79 and from this present a picture of the evolution of amphibolurine dragon lizards. Across  
80 the dragon body, many traits show temporally and phylogenetically heterogeneous  
81 evolutionary histories. Those traits with evidence of varied evolutionary processes often  
82 exhibit large shifts in trait changes coincident with new morphologies. These  
83 morphological jumps are better described by biased directional changes which suggest  
84 selection, rather than increased evolutionary rates. Lastly, we identify that the  
85 diversity of forms of Australian dragons likely evolved from generalist ancestors which

fill space in the adaptive surface and act as intermediates connecting an otherwise patchy landscape.

## Materials and Methods

### *Taxon Sampling*

We assembled a sequence-capture dataset across 309 amphibolurine dragon lizards representing 120 of 136 currently recognized species, with a focus on Australian taxa (115 of 117 spp.). This sampling covers all 16 genera and many recognized subspecies (Table S1). We included outgroup representatives from all agamid subfamilies and used tuatara (*Sphenodon punctatus*) and chicken (*Gallus gallus*) to root the tree (368 total samples).

### *Molecular Data Collection and Processing*

Molecular sampling implemented the Squamate Conserved Loci (SqCL) kit (Singhal et al. 2017), which comprises ~5,000 ultra-conserved elements (UCEs), ~400 anchored hybrid enrichment loci (AHEs), and ~40 legacy genes commonly used in squamate molecular phylogenetics. Sample collection and laboratory preparation, including extraction, shearing, size selection, library generation, and hybridization capture were completed as part of the Australian Amphibian and Reptile Genomics initiative (AusARG) under the Phylogenomics Working Group following the protocol outlined in Tiatragul et al. (2023).

Raw sequence reads are available from the Bioplatforms Australia Data Portal (<https://data.bioplatforms.com/organization/ausarg>). We processed raw sequence data using the *pipesnake* workflow (Brennan et al. 2024). A list of all software and versions used is included in the Supplement. In brief, the pipeline concatenates individual read files, then removes duplicate reads via BBMAP (Bushnell 2014), trims adapters and barcodes with TRIMMOMATIC (Bolger et al. 2014), identifies read pairs with PEAR (Zhang et al. 2014), removes off-target reads with BBMAP, assembles reads to contigs with SPAdes (Prjibelski et al. 2020), maps contigs to targets with BLAT (Kent 2002) and extracts the best hit for each target, carries out preliminary alignments with MAFFT (Katoh & Standley 2013), before refining the alignments with

GBLOCKS (Talavera & Castresana 2007), estimates locus trees with IQ-TREE2 (Minh et al. 2020), and a species tree with weighted ASTRAL hybrid (Zhang & Mirarab 2022). *pipesnake* is a highly reproducible workflow that provides consistent results with little user input.

### *Phylogenetic Analyses*

We estimated individual genealogies for our sequence-capture data (n=5441) under maximum-likelihood in IQ-TREE2 allowing the program to assign the best fitting substitution model using ModelFinder (Kalyaanamoorthy et al. 2017), then perform 1,000 ultrafast bootstraps (Minh et al. 2013). We then estimated the species tree using the coalescent-consistent methods wASTRAL-hybrid and ASTRAL-IV, using IQ-TREE2 gene trees as input. We used two ASTRAL methods to take advantage of the way wASTRAL-hybrid weights branch lengths and support values in estimating the species tree, and how ASTRAL-IV allows multiple individuals per species and estimates both internal and terminal branch lengths in substitutions-per-site (as opposed to coalescent units for internal branch lengths and static terminal branch lengths in wASTRAL). To quantify topological signal from individual gene trees we calculated gene concordance factors using IQ-TREE2 and focused on intergeneric relationships using a single representative for each genus.

### *Divergence Dating*

To estimate divergence times among taxa we applied a series of fossil and secondary calibrations in MCMCTree (Rannala & Yang 2007) as outlined in the Supplement and Table S2. We started by trimming our ASTRAL tree down to a single representative for each ingroup species or subspecies for input. We reduced our molecular data to exonic markers in the AHE loci, then estimated raw genetic distances from alignments to use as a proxy for evolutionary rate. We removed the fastest 5% and slowest 5% of loci to avoid issues with extreme rate heterogeneity, removed third codon positions from all loci, then partitioned the remaining loci into three partitions using AMAS (Borowiec 2016).

For each partition we ran MCMCTree with `usedata = 3` to get the approximate likelihoods and branch lengths using *baseml* (dos Reis & Yang 2011), then concatenated

the out.BV files together. We then ran four replicate MCMCTree analyses on the gradient and Hessian (in.BV file; *usedata* = 2), each for 20k burnin generations before collecting 20k samples at a sampling frequency of 100 generations (2,020,000 total generations). We compared mcmc files for stationarity and convergence (ESS of all parameters > 200), combined them using logCombiner, and used this combined mcmc file to summarize divergence times on our tree (*print* = -1 in .ctl file). To validate our priors we ran an additional analysis (*usedata* = 0) to run explicitly from the prior calibrations and determine our effective priors for comparison against our posterior age estimates. We then plotted the applied priors against effective priors (priors as a result of multiple interacting priors from *usedata* = 0) and posterior estimates to ensure appropriate behavior of the MCMCTree analyses (Fig.S1).

To take advantage of all available morphological and phylogenetic information we incorporated three additional New Guinean *Hypsilurus* species into our dated tree used for trait evolution analyses. *Hypsilurus godeffroyi*, *H. papuensis*, and *H. nigrigularis* were added to our MCMCTree output using *bind.tip* in *phytools* (Revell 2024), based on the topology and ages estimated from a recent phylogenomic investigation of Squamata (Title & Singhal et al. 2024).

### *Morphological Data Collection*

We collected 19 linear measurements for 128 amphibolurine lizard species from 482 museum samples ( $\bar{x}$  = 5 per spp., min. = 1, max. = 8). Linear measurements were collected by one author (IGB) using Mitutoyo digital calipers (product 500-763-20). These measurements aimed to capture the gross morphology of the lizard body plan and are distributed across the head, body, limbs, and tail (Fig.S2). Definitions of trait measurements and adjustments are summarized in Table S3. Data processing and analyses were carried out in R (R Core Team 2024).

### *The Evolution of Morphological Diversity*

To identify the mode of individual morphological traits we fit a series of models ranging from an unbiased random walk to rate-variable and trended. The most basic model—Brownian Motion (BM)—allows phenotypes to evolve through incremental random change. The most complex—*BayesTraits* V4's fabric model (Pagel et al. 2022)—also

follows a process of gradual change, but allows rates to shift at discrete points (changes in *evolvability*,  $v$ ) on the tree and allows traits to change rapidly along individual branches through directed evolution (*trends*,  $\beta$ ). Using *BayesTraits V4* we fit these models and their derivatives (*fabric* with no  $v$  parameter, *fabric* with no  $\beta$  parameter) and estimated their marginal likelihoods using a stepping-stone sampler (500 stones each for 5,000 generations).

*BayesTraits V4* implements a reversible-jump MCMC sampler, which we specified to run for 100 million generations with 10 million generations of burnin. We summarized the output to check for convergence with a custom script *Scripts/processBTVarRates.R*, and verified that all parameters had reached effective sample sizes (ESS)  $> 200$ . To verify model fit and consistency among runs we ran four separate runs for each trait. Individual model outputs (...*VarRates.txt*) were summarized using the *FabricPostProcessor* software and independent runs were combined using *MergeFabric*. Significant evolvability ( $v$ ) and trend ( $\beta$ ) shifts had to occur in all four runs.

To track trait values at internal nodes we logged values from the MCMC chain using the *AddTag* and *AddMRCA* features in *BayesTraits* by generating custom control files using functions defined in the Supplement. We also used this script to generate reasonable priors on the root state and rate by fitting a single rate BM model using *GEIGER* (Pennell et al. 2014). We summarized posterior estimates of ancestral trait values under varied models using custom scripts included in the Supplement. To track the evolution of dragon morphospace through time we reduced observed and estimated ancestral values to three principal component axes and fit multidimensional hypervolumes using *hypervolume* (Blonder et al. 2018). We then extracted the volume and density of hypervolumes at 0.5 million year intervals. To understand morphological distances between observed and estimated (ancestral) taxa/optima we measured Euclidean distances. We visualized functional morphological spaces using the package *funspace* (Pavanetto & Puglielli 2024)

To identify adaptive peaks across the multidimensional landscape (i.e., morphological regimes) we used an OU-based method that accounts for correlation among traits



(*PhylogeneticEM*; Bastide et al. 2018). We used two different datasets as input. The first included all 19 non-overlapping morphological traits. Due to the strong correlation of some traits (Fig.S3) we generated a second dataset by reducing dimensionality through principal components analysis (PCA) and choosing the top six principal component axes which accounted for >90% of the cumulative variance, where each component explained >2%. We fit the models across a number of shift values (K=0-15) and a grid of 30 alpha values (a=0-5) to both datasets. For consistency, we fit a variety of additional schemes to test the reliability of our results, and those are explored further in the Supplement. After identifying the preferred number of optima (either 5 or 12; see Results; also called regimes) we used these as discrete characters for *RandomForest* (Liaw & Wiener, 2022) analysis to categorize ancestral taxa according to contemporary optima. Assigning species to ecological guilds is fraught with subjectivity so we relied on our morphological regimes to identify clusters of species that map loosely to existing ecological categorizations (e.g. arboreal, terrestrial) following the discussion of these species in Melville & Wilson (2019). RandomForest confusion (error) rates for almost all contemporary optima were sufficiently low (<10%) and so we predicted the morphological regime of ancestral taxa (nodes) based on trait values estimated by the best fitting model for each trait.

## Results

### *Molecular Data Collection and Processing*

Sequence capture using the SqCL kit resulted in assembly of 5441 targets. New sampling recovered a median of 5118 loci, with a concatenated and aligned sequence length of >6 Mbp (Fig.S4). Additional sequence statistics are included in the Supplement.

### *Phylogenetic Analyses*

Coalescent-consistent topologies estimated by wASTRAL-hybrid and ASTRAL-IV are well resolved with high support across most branches of the tree, including good resolution among genera and major clades (Fig.1; Fig.S5). Internal branches separating the Australian genera are short and consecutive rapid splits show high levels of incomplete lineage sorting resulting in low gene concordance factors (Fig.S6). This is

notable in the positions of the *Moloch/Chelosania* and *Lophosaurus* clades and placement of *Tropicagama*. Additional areas of conflict are limited to interspecific placements of the *Ctenophorus fordii* group, the *Pogona minor* group, and the *Diporiphora pallida* group. In agreement with a recent study (Bruton et al. 2025) we find *Ctenophorus* (*Cryptagama*) *aurita*—a highly morphologically derived lineage—nested within *Ctenophorus*. Our phylogeny also supports the assignments of a number of frequently confused arid and savannah species, upholding the genera *Amphibolurus*, *Gowidon*, *Lophognathus*, and *Tropicagama*. We also provide strong evidence that unites *Rankinia*—the world’s highest latitude dragon—with *Pogona*. Beyond the Amphibolurinae, we also provide a strongly supported estimate of subfamilial relationships in the Agamidae. We recover a sister relationship between the Agaminae and Draconinae, which together are the sister to the Amphibolurinae. The next closest relatives are the Hydrosaurinae, followed by the Uromastycinae, and lastly the Leiolepidinae (Fig.1)

#### *Divergence Dating*

Amphibolurines appear sometime in the late Cretaceous (~75 mya), separating from their sister the Agaminae/Draconinae. The crown split among amphibolurines does not occur until much later, at the Eocene/Oligocene boundary ~34 mya. Cladogenetic events occur rapidly at the base of the amphibolurine tree, with the major splits among Australian groups all occurring between 30-25 mya. With the exception of the clade comprising *Chlamydosaurus*, *Lophognathus*, and *Amphibolurus*, all extant genera were established by the mid-Miocene ~15 mya. Rapid speciation events towards the base of the amphibolurine tree obscure some relationships, likely a result of quick successive splits in <600 ky (Fig.1).

#### *Phenotypic Evolution*

Of 19 morphological traits, 10 are best fit by the rate-variable and trended model from *fabric*, including the summary trait encapsulating size (Table S4). The remaining nine traits are best fit by a random walk model (Brownian Motion). Traits with greater variance and disparity are more likely to fit the *fabric* model (Fig.S7). Ancestral trait values for the 10 traits best fit by *fabric* were extracted and summarized from the mcmc output files. Ancestral trait values for the remaining nine traits were estimated

under Brownian Motion. This provided a complete trait matrix for living and ancestral species which we used to quantify ancestral morphologies. Morphospace shows a heterogeneous pattern of expansion with a steep increase from 30-20 million years, before a period of little expansion from 20-10 million years, and another increase in volume from 10 million years to present (Fig.S8).

Multi-optima OU models identify either 5 or 12 morphological regimes. We refer to these regimes by the primary ecological habits of their members (arboreal, terrestrial, generalist) or the clade to which they belong (*Tympanocryptis*, *Moloch*), and consider how these morphological assignments map to ecology in the Discussion. Our multi-optima solutions are nested with the same 5 optima identified in the more conservative model and in the liberal 12 optima model. These optima correspond to arboreal taxa at the base of the tree (*Hypsilurus*, *Lophosaurus*, *Chelosania*), two separate terrestrial clades (*Tympanocryptis*, *Ctenophorus*), a generalist Australian semiarboreal group (*Amphibolurus*, *Gowidon*, *Intellagama*, *Tropicagama*, *Lophognathus*, *et al.*), and the unique *Moloch* (Fig.2; Fig.S9). More liberal models add optima which largely correspond to genera (e.g. *Diporiphora*, *Pogona* + *Rankinia*) and outlier species (*Chlamydosaurus kingii*, *Cryptagama aurita*, *Diporiphora superba*) and optimally identify 12 peaks (Fig.S10). These clusters are largely visible when looking at raw morphological distances among taxa (Fig.S11).

In both optima scenarios ( $k = 5$ ,  $k = 12$ ), RandomForest predictions suggest an arboreal-type ancestor for the Amphibolurinae with some uncertainty ( $k = 5$ , 66% assignment to arboreal;  $k = 12$ , 58%). The core Australian amphibolurine ancestor (most recent common ancestor of *Intellagama* and relatives) is estimated to fit the regime comprising semiarboreal generalists, however, its immediate ancestor is estimated as fitting the arboreal regime. The amphibolurine MRCA is estimated to have trait values most similar to *Chlamydosaurus*, *Intellagama*, and *Physignathus* (Fig.S11,S12).

## Discussion

The diversity of organismal forms in nature are not distributed evenly across the possible phenotypic space. Instead, observed phenotypes often cluster in discrete regions of morphospace, a result of genetic, functional, and/or developmental constraints (Deline et al. 2018). These clumps of morphologically similar organisms identify peaks in the adaptive landscape. Through time, the adaptive landscape may change as conditions vary and species go extinct, persist, and proliferate. The invasion of a new geographic region provides us the opportunity to observe how the adaptive landscape evolves, and to identify the tempo and mode with which new regions of the landscape become populated. Amphibolurinae dragon lizards are an ideal system to evaluate this. Our findings suggest that dispersal of dragon lizards into Australia facilitated a marked expansion in the morphological landscape. This exploration was driven first by a transition from an arboreal to a generalist ancestor and later into specialized ecomorphologies. Major morphological transitions were aided by focused evolution resulting in the rapid change of traits.

### *Phylogenomics of the Amphibolurinae*

Dragon lizards (Agamidae) are a charismatic and diverse group of ~600 species found across Africa, Asia, and Oceania. They are diurnal and often brightly colored and territorial, making them visible and familiar. One subfamily, the Amphibolurinae, extends out of Asia into Australia and New Guinea. Here they reach their greatest ecomorphological extremes, ranging from burrowing species that live along the salt-crusted edges of desert lake-beds to semiaquatic species that patrol the eastern watercourses. While some species are familiar, such as the bearded dragons and frilled-neck lizards, to date, phylogenetic understanding of the group has been limited in genetic scope and focused within genera (Macey et al. 2000; Melville et al. 2001, Hugall et al. 2008; Shoo et al. 2008; Melville et al. 2018; Chaplin et al. 2020; Fenker et al. 2024). Our new sequence-capture dataset provides a well-supported estimate of the relationships among all 17 amphibolurine genera and more than 88% of described species.

Relationships among some (Streicher et al. 2016; Burbrink et al. 2020; Title et al. 2024) or all (Welt & Raxworthy 2022) agamid subfamilies have been estimated from different phylogenomic datasets, but have not previously been discussed. Our topology differs from that of Welt & Raxworthy (2022) in the placement of the Leiolepidinae and Uromastycinae at the base of the tree, and the stepwise (rather than sister) relationship between the Hydrosaurinae and Amphibolurinae. The topology we present has biogeographic implications, suggesting an Asian and not African origin for the group. This is further supported by fossil evidence of the Priscagamidae which were stem-acrodonts of east Asia, and the ~99 myo *Protodraco* from Myanmar (Wagner et al. 2021) which is potentially the oldest known acrodont. The debate over an Asian or African origin of agamids is mirrored in other Australian squamate groups such as pythons (Esquerre et al. 2020), monitor lizards (Brennan et al. 2021), and elapid snakes (Keogh 1998). One possible explanation for differences in the subfamily topology is the expanded molecular dataset presented here. Reanalyzing a UCE-only dataset however, returns a topology identical to our SqCL estimate, suggesting other factors (e.g. alignment parameters, substitution models) are likely causing the differences in topology.

While the Amphibolurinae as a group date back to the Cretaceous, their living diversity is less than half that age. The split between the sole Asian species *Physignathus* and the remaining Australo-Papuan diversity occurred around the Eocene/Oligocene transition, and was closely followed by rapid diversification over the next ten million years (Fig.1). This is consistent with paleontological evidence from Australia which suggests fossils assignable to *Intellagama* are relatively common in the early-to-middle Miocene deposits of the Riversleigh World Heritage Area (Covacevich et al. 1990). The rapid divergence of Australian species from their forest-dwelling relatives in New Guinea resulted in a series of very rapid branching events which can prove challenging for phylogenetic methods. These deep and rapid splits occur over just a few hundred thousand years and highlight a period of dramatic ecomorphological change. Following this period of radiation, the diversification of the group is far slower, more homogeneous, and dictated by three major groups: *Ctenophorus* (41 spp.), *Diporiphora* (28 spp.), and *Tympanocryptis* (26 spp.). This pattern of speciation slow-

down is consistent with theory around adaptive radiations and dispersal into new regions (Harmon et al. 2010; Schluter 2000; Simpson 1944; Yoder et al. 2010).

### *Mapping Morphology to Ecology*

The adaptive landscape of amphibolurine dragons is dispersed and patchy, with peaks that largely correspond to recognized genera. Connecting these peaks are generalist semiarboreal forms that appear to facilitate the transition into more extreme morphological space and new ecologies. Obvious phenotypic peaks relate to strongly arboreal (*Hypsilurus*, *Lophosaurus*) and terrestrial species (*Tympanocryptis*, *Ctenophorus*). However, intermediate forms that are adept at both running and climbing fill the morphological space and unite the more disparate peaks of the landscape (*Amphibolurus*, *Gowidon*, *Lophognathus*, *Tropicagama*, et al.). These generalist taxa are either lumped under a single broad adaptive peak (when  $k=5$  optima; Fig.S9) or two peaks (when  $k=12$  optima; Fig.S10). This is important because these intermediate morphologies appear common (~50% of species richness), are distributed across the entire continent in all habitat types, and provide a theoretical link between more extreme morphological forms. The idea of generalists as a bridge between morphotypes is not exclusively a reflection of how we generate morphospaces. In dragon lizards this process is informed by the branching pattern of the phylogeny. Specialist forms often descend from morphologically intermediate ancestors, and in some cases are nested deeply within generalist clades. For example the stout rock-dwelling *Diporiphora bennetti* and gracile hummock grass living *Diporiphora adductus* likely both evolved from a more typical amphibolurine morphology seen in their closest relatives.

Linking morphology to ecology however, is not always so clear. This may be the result of a many-to-one mapping where varied morphologies enable the same ecology (Wainwright et al. 2005; Moen 2019). For example, taxa such as *Lophosaurus*, *Chelosania*, and *Diporiphora superba* are all obligately arboreal and highly specialized dragons, however, these taxa map to either two or three discrete adaptive zones (Fig.2) and use arboreal spaces differently. *Diporiphora superba* is an extremely gracile species with a long tail, small head, and long slender limbs that it uses to move through shrubs. *Lophosaurus* species similarly have long tails and limbs, but have large heads

and deep, laterally compressed bodies and generally perch vertically on tree trunks. *Chelosania* also show a narrowing of the body but have short sturdy limbs and a relatively short tail for a species that is almost never found outside of the canopy where they often use horizontal branches. In this situation, convergence on a specialized lifestyle is met with only incomplete morphological similarity. This may be due to a number of reasons including phylogenetic inertia resisting selection (Blomberg & Garland 2002). This idea is relevant when considering the ecology of the ancestral amphibolurine. Our analyses suggest this ancestor was likely morphologically similar to the arboreal *Lophosaurus* and *Hypsilurus*, but also to *Physignathus* and *Intellagama*—two species that are considered semiaquatic (Fig.SX12). These last two species are similar enough that they were considered congeneric for over 150 years and are often called “water dragons”. Despite their preferred habitat, they fit most morphological descriptors of a tree-living dragon. We flag this to note the imperfect mapping of morphology to ecology and uncertainty in estimating ancestral states.

#### *The Evolving Adaptive Landscape*

The transition from wet closed-canopy rainforests in Asia and New Guinea towards new and different environments in Australia presents a prime case for ecological opportunity (Collar et al. 2010; Gray et al. 2019a). Among the newly available habitats, dragons encountered sparse open forests, grasslands, sandy and stony deserts, and rocky escarpments, which are all but absent across Malesia. By expanding their geographical range, dragon lizards also extended the adaptive landscape to enable new forms that took advantage of these habitats (Yoder et al. 2010). This extension provided opportunity for new peaks located in distant regions of morphospace. To traverse that space however, required deterministic trends in trait evolution that suggest selection on individual or suites of traits (Figs.3,4). In dragon lizards, this may have first resulted in a transition from an arboreal form to a generalist form. Our analyses indicate that this occurred rapidly and dramatically, resulting in a multivariate shape change dozens of times greater than expected (Fig.3 highlight 5). The resulting form likely had shorter limbs and tail, a wider body, and shorter snout as it spent less time in the trees (Fig.4). From generalist forms amphibolurines were able to further explore morphological extremes. This includes repeated transitions

towards small-bodied terrestrial forms (*Ctenophorus aurita*, *Rankinia*, *Tympanocryptis*), (Fig.4), and moves back towards elongate arboreal forms (*Diporiphora superba*, *Chlamydosaurus*). In this way, generalists negate the need to cross wide fitness valleys in the adaptive landscape. Instead, species can explore across ridges or broad fitness peaks to reach distant morphospaces. This provides more evidence that transitions across the landscape from specialist to specialist are uncommon and likely require an intermediate form.

In our investigation across the dragon lizard body plan, we identify varied modes of evolution among and within traits. In the simplest sense, the evolution of dragon morphology is dictated by both a gradual diffusion process away from stable peaks and infrequent shifts in the evolutionary rate or trait mean. Perhaps most exciting about these findings is how rare these shift events are. To explain the disparate morphological landscape of dragons less than 10% of branches need multivariate trait change that exceeds Brownian expectations. We can see this when looking across the morphospace, where discrete regions are heavily occupied (Fig.1). These high density areas indicate slow evolutionary rates or constrained evolution (i.e. Ornstein Uhlenbeck), as has been previously identified in *Diporiphora* (Smith et al. 2010). Stable peaks populated by many closely-related species highlight diffusion as the most frequent pathway for change among species. In comparison, rare evolutionary shifts are concentrated around changes among adaptive zones. These shifts are nested and temporally staggered resulting in a dynamic adaptive landscape that does not reflect the archetypical tempo or mode of an adaptive radiation. This complex mosaic of evolutionary modes helps to reconcile Simpson's idea of quantum evolutionary change (few, extreme changes) with Darwin's ideas of gradualism (frequent, small changes) (Simpson 1944; Charlesworth et al. 1982).

The morphological evolution of dragon lizards has been a heterogeneous process, varying temporally, phylogenetically, and across traits. Broadly, dragons have gone through periods of early and late expansion in the morphological hypervolume, bookending a period of little innovation during much of the Miocene (Fig.S8). Looking across all species, we identify that the primary axes for variation are through change in absolute size and tail length (Fig.S7). This is immediately apparent when comparing



large tree dragons (*Hypsilurus magnus*: SVL >200 mm, tail length >600 mm) to pebble-mimicking dragons (*Ctenophorus aurita*: SVL <40 mm, tail length <35 mm; *Tympanocryptis cephalus* group: SVL <60 mm, tail length <90 mm). Elaboration in size and tail length beyond other traits is a pattern seen in other squamate clades (Brennan et al. 2024; Meiri 2010), but dramatic changes are not limited to these axes. Instead, amphibolurines show exceptional variation in many traits and greater than expected diversity relative to other iguanians (Gray et al. 2019a; Gray et al. 2019b). Most trait trends appear associated with habitat type (Thompson & Withers 2005; Collar et al. 2010), such as broader heads and wider bodies in terrestrial groups or longer limbs and snouts in arboreal species. But others are harder to quantify and likely associated with defense or communication, like the frill of *Chlamydosaurus* or fixed and erectable crests in many species. Harder yet to explain is the tremendous novelty of *Moloch*, a lizard commonly called the thorny devil for the keratinous spines that cover its body. Despite their familiarity, *Moloch* remain enigmatic in many ways. They likely pre-date the Australian deserts in which they wander (Pepper & Keogh, 2021). They exclusively eat ants. And they have undergone such a profound evolutionary modification that they are nearly unrecognizable as agamids. In expanding into this new adaptive zone, the thorny devil has stretched the morphological space, representing just one of many exciting peaks in the landscape of dragon lizards.

## Conclusion

The adaptive landscape is a popular metaphor for linking form to function and contextualizing organismal diversity. For a long time we have focused on studying the peaks, but it has been difficult to imagine how species have traversed the landscape to establish new adaptive zones. Our investigation into the evolution of the morphological landscape in amphibolurine dragon lizards emphasizes the importance of generalist forms in connecting discrete peaks. While the ancestral amphibolurine was likely an arboreal dragon, the diversity of Australian forms were only realized following strong directional changes to a labile generalist form. As others have noted (Collar et al. 2010; Gray et al. 2019a; Gray et al. 2019b), this was likely driven by ecological opportunity in the form of a range of new habitats after landing in Australia. As a result, Australian

dragons represent one of the continent's most impressive adaptive radiations. Importantly, this system shows how the adaptive landscape itself can change and grow, expanding its borders and altering its topography in response to new opportunities.

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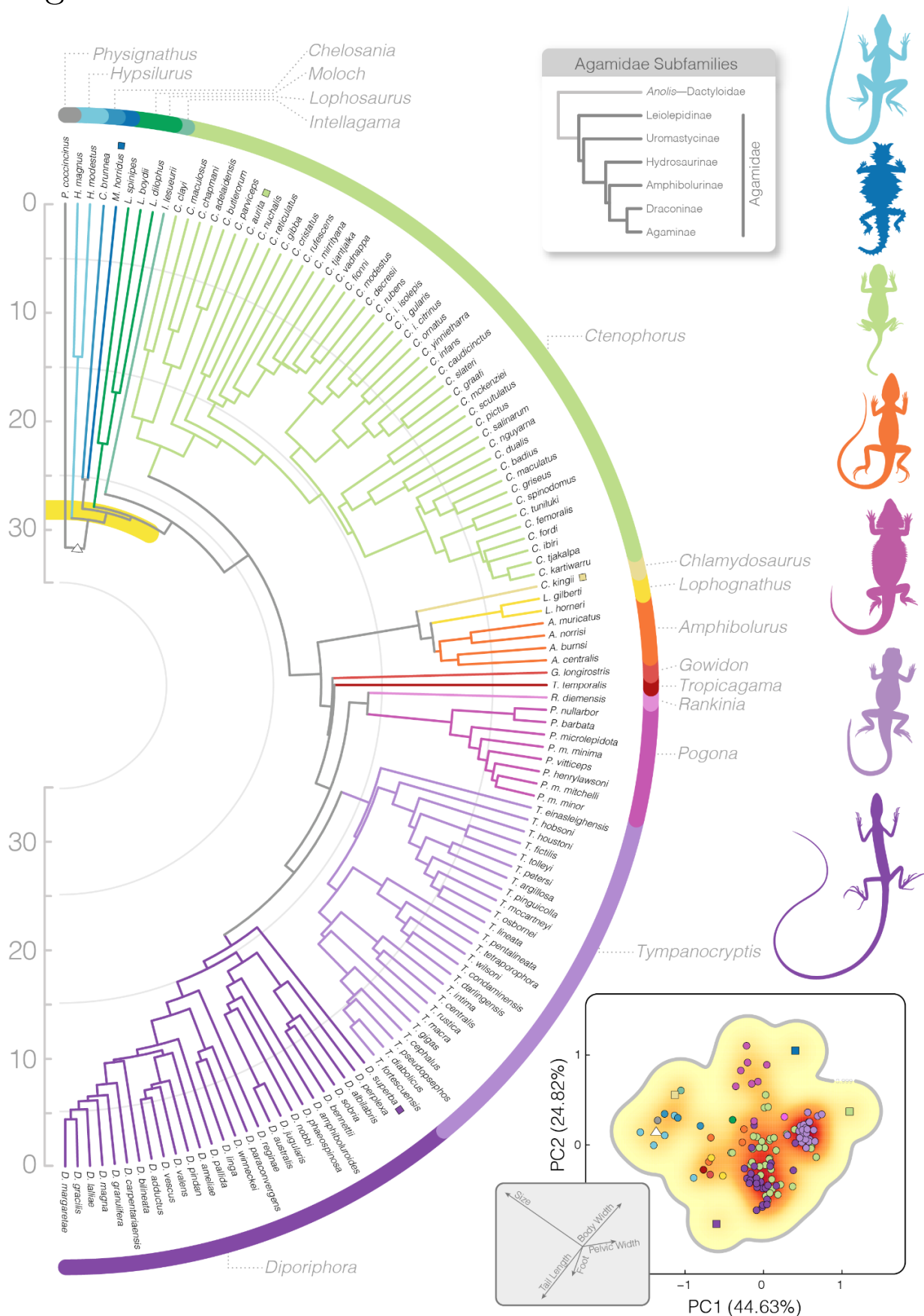


Figure 1. Species-level timetree of the Amphibolurinae, color-coded by genus. The ASTRAL species tree time-calibrated with MCMCTree shows a rapid Oligocene divergence of most major amphibolurine groups. A yellow band highlights the series of rapid splits early in the history of this group. Inset bottom right shows the spread of species in two-dimensional morphospace (also colored by genus) and primary axes of variation. *Diporiphora* (dark purple) and *Tympanocryptis* (light purple) highlight dense clusters of morphospace, contrasting with morphological outliers indicated by squares in the morphospace and on the tree (*D. superba*, *M. horridus*, *C. aurita*). The estimated root morphotype is indicated by a triangle. Inset top right shows relationships among agamid subfamilies and color-coded dragon drawings at right (not to scale) highlight some of the morphological diversity of this group. White circles on the tree denote local posterior probabilities  $<0.95$ .

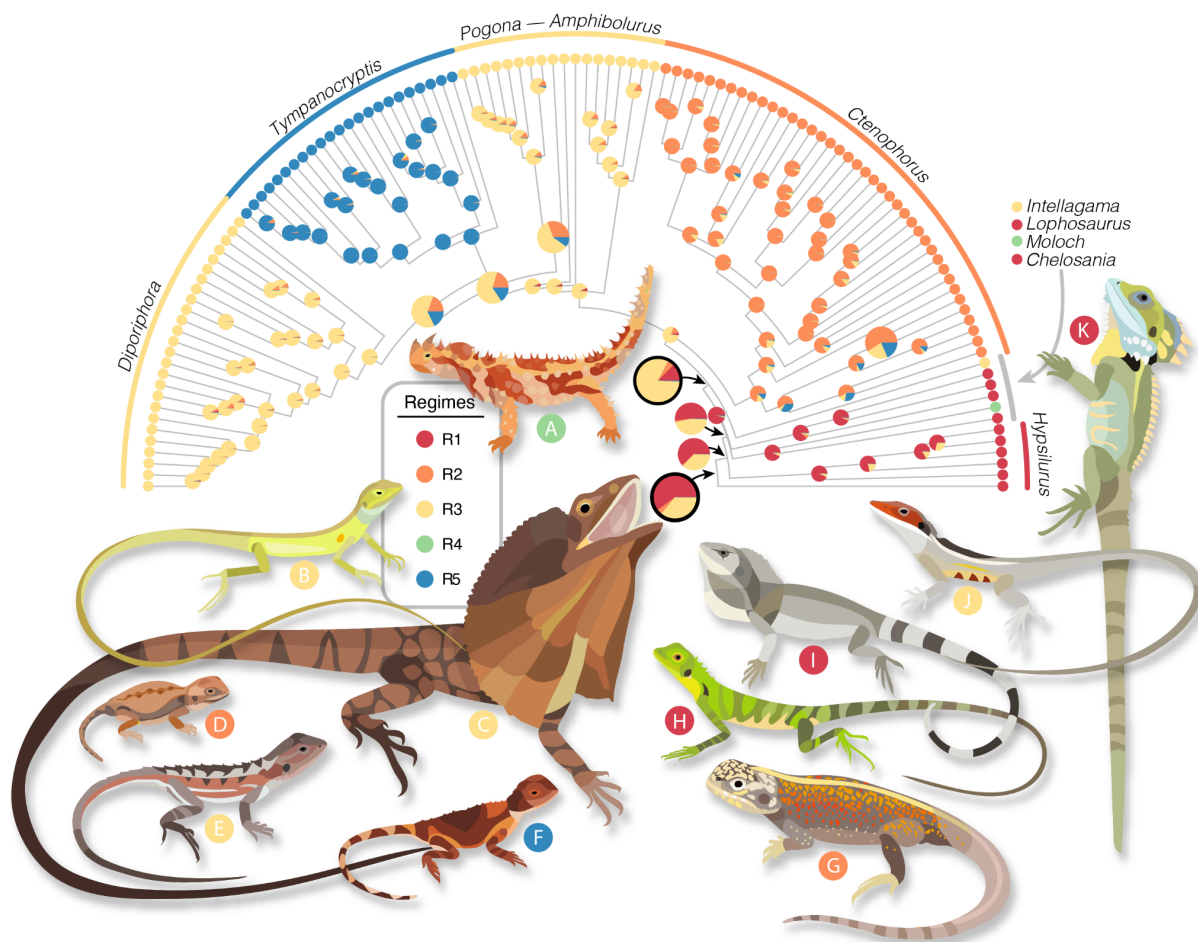


Figure 2. The adaptive morphological zones of amphibolurine dragons highlight a diversity of forms. Colored regimes were identified under a multi-optima OU model in *PhyloEM* and applied to ancestral taxa using *randomForests*. The tree shows the preferred 5 regime model estimated from all 19 size corrected morphological traits and likelihoods for ancestors as estimated by *randomForest*. Two regimes (blue, orange) map to obligately terrestrial groups. The red regime highlights primarily arboreal species and the morphologically similar *Physignathus*. Yellow indicates a diverse clade of primarily generalist species. The amphibolurine most recent common ancestor (MRCA) is estimated as a *Hypsilurus*/*Lophosaurus*-like arboreal dragon and the Australian MRCA is estimated as a semiarboreal generalist lizard (both indicated with black outlined pie). Illustrated species are (A) *Moloch horridus*, (B) *Diporiphora superba*, (C) *Chlamydosaurus kingii*, (D) *Ctenophorus aurita*, (E) *Rankinia diemensis*, (F) *Tymanocryptis pseudopsephos*, (G) *Ctenophorus reticulatus*, (H) *Hypsilurus modestus*, (I) *Chelosania brunnea*, (J) *Gowidon longirostris*, (K) *Lophosaurus boydii*.

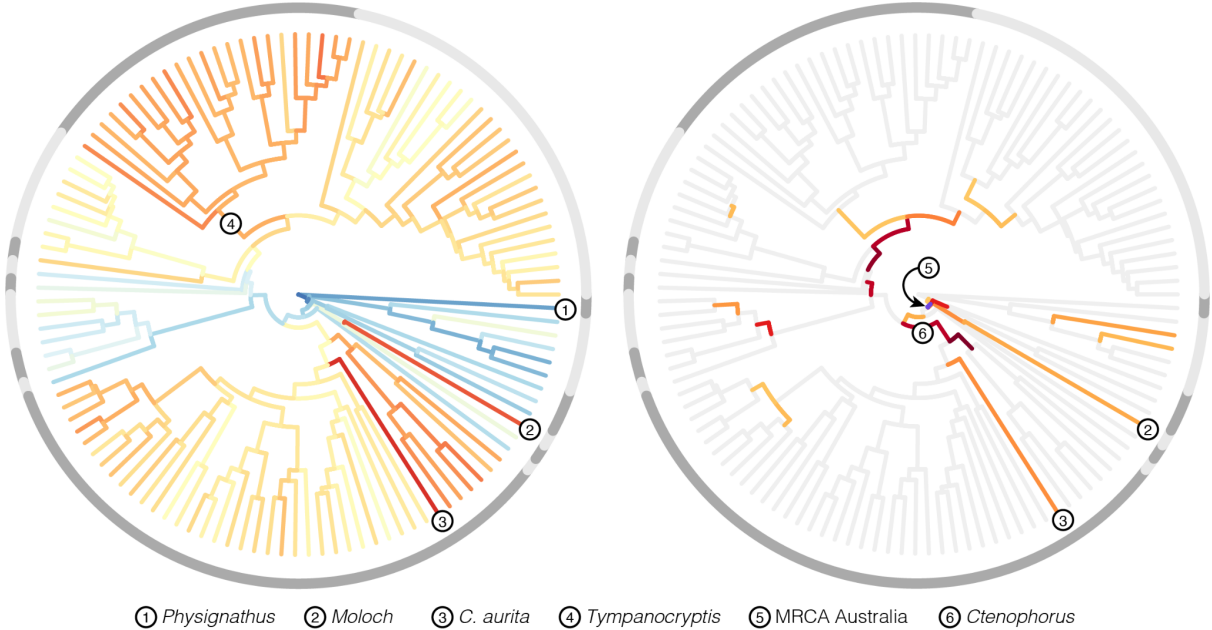
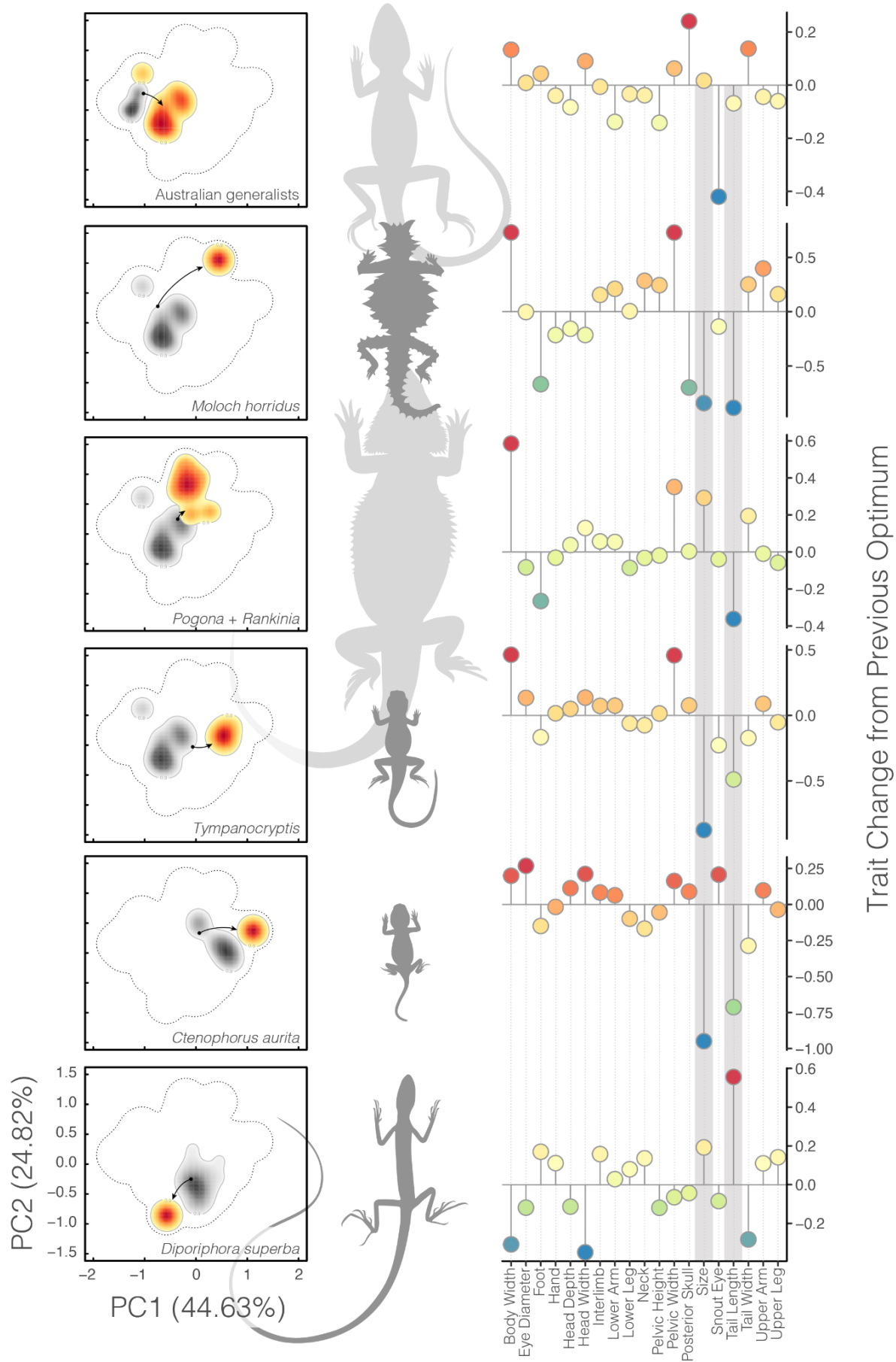


Figure 3. Major shifts in morphologies occur as directional evolutionary changes that are greater than expected. Left, morphological innovation across the dragon tree, with warm colors indicating greater multivariate Euclidean distance from the amphibolurine most recent common ancestor, and cooler colors indicating greater similarity. Grey shading in outer circles delineates genera. Right, the position and strength of directional changes that exceed multivariate shape change under the null evolutionary model. Circle number 5 indicates the branch leading to the Australian radiation of dragon lizards and denotes a 26-fold increase over the expected amount of morphological change. This very short branch accounts for a paradigm shift in the evolution of amphibolurine lizards away from an arboreal ancestor towards a more generalist morphology.



567 Figure 4. Movement among optima occurs via changes in different suites of traits. Plots  
568 in the left column visualize the shift from the immediately ancestral optimum (grey  
569 shading) to a new optimum (warm shading) represented in two dimensional space.  
570 Lizards at center illustrate the morphological extremes of new optima. Plots at right  
571 indicate how individual traits changed in evolving from the previous optima to current.  
572 Grey bars highlight the two most variable traits: size (a composite of the geometric  
573 mean of all trait measures) and tail length.



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