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Evolutionary biology

Convergent evolution of tail spines in squamate reptiles driven by microhabitat use

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The repeated evolution of convergent or analogous traits is often used as evidence for adaptive evolution. Squamate reptiles show a high degree of convergence in a variety of morphological traits; however, the evolutionary mechanisms driving these patterns are not fully understood. Here, we investigate the evolution of tail spines, a trait that evolved multiple times in evolutionarily independent clades of lizards. Taking a comparative phylogenetic approach, we use 2877 squamate species to demonstrate that the evolution of spiny tails is correlated with microhabitat use, with species that live in rocky habitats significantly more likely to have evolved spiny tails. In the light of previous behavioural observations, our results suggest that spiny-tailed lizards have an advantage in rocky habitats through predation avoidance, where tail spines are used to prevent extraction from rocky crevices. In concordance with previous research on lizard body armour, our results suggest that the evolution of tail spines is coupled to both a rock-dwelling lifestyle and predator avoidance strategies, and highlight a complex interplay between different selective pressures on the evolution of defensive morphologies in reptiles.

1. Background

Understanding how selective pressures have shaped the extensive phenotypic diversity of life is a fundamental goal in evolutionary biology. In a macroevolutionary context, multiple, independent origins of analogous or homologous traits are often used as evidence for adaptive evolution [1]. Linking convergent or functionally similar traits to species' ecology can shed light on shared environments associated with their repeated evolution.

The evolution of defensive morphologies (e.g. spines, thickened keratinous scales, osteoderms) has been linked to predation pressures in a diverse array of organisms, including mammals, fish and reptiles [1–7]. However, the evolution of body armour in cordylid lizards has previously been linked with arid environments, rather than being a direct result of predation pressure [8]. While predation pressure may not be directly correlated with the evolution of armour, the interaction between both environment and predation likely plays a key role [9].

Lizards have evolved analogous keratinous or osteodermal tail spines in several evolutionarily independent clades, including Cordylidae, Agamidae, Iguanidae, Varanidae and Scincidae [8,10–13]. The apparent convergence in these defensive morphologies, which we collectively refer to as 'spiny tails' herein, is striking. In contrast to body armour, tail armour has not previously been extensively studied (but see [14]). A study by Arbour & Zanno [14]

found that in amniotes, the evolution of tail weaponry is associated with large body size and active tail-lashing behaviour. Although some spiny-tailed lizards engage in active tail-lashing [15], tail spines have mainly been documented to act as part of a passive anti-predation strategy, by preventing extraction from rocky crevices (e.g. [16,17]). The results of a behavioural study by Cooper *et al.* [15] also suggest that the enlarged tail spines of rock-dwelling species may be especially advantageous to avoid predation in crevices.

Although interspecific differences regarding anti-predation behaviour have been observed [15], it is possible that the repeated evolution of spiny tails, and subsequent defensive behaviours, have evolved in response to similar ecological pressures experienced by species inhabiting rocky (saxicolous) habitats. Here, we use a time-calibrated phylogeny of 2877 species of squamate reptiles and a phylogenetic comparative approach to test for an association between the evolution of spiny tails and microhabitat use, as well as for differences in body size and changes in diversification rates associated with the evolution of spiny tails.

2. Material and methods

(a) Phenotypic and microhabitat data

We assembled a dataset for squamates consisting of maximum body sizes (log10 values from [18]) and microhabitat association (from [19] and electronic supplementary material, references). In an effort to reduce functional redundancy, we recoded the microhabitat association for each species into one of eight categories (aquatic, terrestrial/aquatic, arboreal, terrestrial, terrestrial/arboreal, terrestrial/saxicolous, fossorial or terrestrial/fossorial). We additionally coded microhabitat as a series of binary traits for each species (see electronic supplementary material, table S1). For each taxon, we then assembled data from the literature (see electronic supplementary material, references) on the presence or absence of a spiny tail, i.e. clearly visible keratinous or osteodermal tail spikes (binary; 0 no spiny tail, 1 spiny tail). In some cases, the presence of tail spines was ambiguous, so we created two versions of the dataset: 'SPINY' and 'SPINY STRICT' (electronic supplementary material, table S1). The latter dataset only included species showing tail scales organized into discrete whorls, with caudal ends of scales possessing clearly visible spines (with a few exceptions; see electronic supplementary material, figure S1 for further explanation). Since snakes do not possess spiny tails, we also reran all analyses with lizards only.

(b) Phylogenetic tree and ancestral state reconstruction

We used a previously published, large-scale phylogenetic tree [20] as the basis for our phylogenetic comparative analyses. Using 14 internal calibration points (following [21]), we dated the tree using a phylogenetic penalized likelihood approach in treePL [22]. We then pruned the tree to only include species for which we obtained microhabitat, body size and spiny tail trait information, with 2877 species retained for downstream analysis.

To reconstruct ancestral states and estimate the number of origins of spiny tails in squamate reptiles, we used stochastic character mapping [23] using the make.simmap function in the R package phytools [24] for both the SPINY and SPINY STRICT datasets. We ran 1000 iterations to obtain a posterior distribution for the timing and number of independent origins of spiny tails.

(c) Comparative analyses

We tested for the phylogenetic signal of spiny tails across all datasets using the D statistic [25] in the R package caper [26].

To test for a correlation between the evolution of spiny tails and microhabitat association in squamates, we used the fitPagel function in phytools with the tail state as the dependent variable. This function tests for correlated evolution between two binary traits [27]. We additionally used phylogenetic ANOVA in phytools to test for significant differences in the evolution of spiny tails across microhabitat categories in which spiny-tailed lizards were present (arboreal, terrestrial, terrestrial/arboreal, terrestrial/saxicolous).

To determine whether body size was correlated with the tail state, we used phylogenetic logistic regression using the R package phylolm [28]. We also used phylogenetic ANOVA to ascertain whether body size differed across either tail states, or across different microhabitats. All resultant *p*-values were corrected for multiple comparisons using a Bonferroni correction.

(d) Diversification rate analysis

To test whether the evolution of spiny tails had an impact on diversification rates, we tested for trait-dependent diversification rate shifts using a Hidden State-Dependent Speciation and Extinction (HiSSE) model [29] in the R package hisse [29]. The precursor to HiSSE, the Binary State-Dependent Speciation and Extinction (BiSSE) model, compares a null model of no diversification rate shifts on the tree, to an alternate model where changes in diversification rates are correlated with an observed character. By contrast, the null model in a HiSSE analysis allows speciation rates to vary on the tree, correlated with a secondary, unobserved character. We compared a model where diversification rates are correlated with spiny tail evolution, to both the HiSSE and BiSSE null models using AIC model selection.

3. Results

(a) Independent evolution of spiny tails in squamates

The posterior distribution of stochastic character mapping recovered a mean of 76.2 transitions between states in either direction (figure 1a), or 48.5 transitions for the SPINY STRICT dataset. Using the primary dataset (SPINY), we reconstructed a posterior mean of 37.9 transitions from non-spiny to spiny and 38.4 reversals from spiny to non-spiny. In the STRICT dataset, the average number of transitions from non-spiny to spiny (mean = 33.3) was much higher than the number of reversals (mean = 15.2). We inferred a negative D statistic for all datasets (electronic supplementary material, table S4), which were significantly different from 1.

(b) The evolution of spiny tails is correlated with a saxicolous lifestyle

In a binary trait coevolution framework, we found a significant correlation between the evolution of spiny tails and association with terrestrial/saxicolous microhabitats across all datasets (figure 1, table 1). In all cases, likelihood-ratio tests suggested that a model of correlated evolution between spiny tails and terrestrial/saxicolous microhabitat performed better than models where these traits evolved independently. In the SPINY dataset, there was also a significant correlation between the evolution of spiny tails and terrestrial microhabitats. In the SPINY STRICT dataset, we found a significant correlation between the evolution of spiny tails and arboreal microhabitats. The results were similar when snakes were excluded (electronic supplementary material, table S2). Pairwise phylogenetic ANOVA comparisons indicated that species inhabiting terrestrial/saxicolous microhabitats were

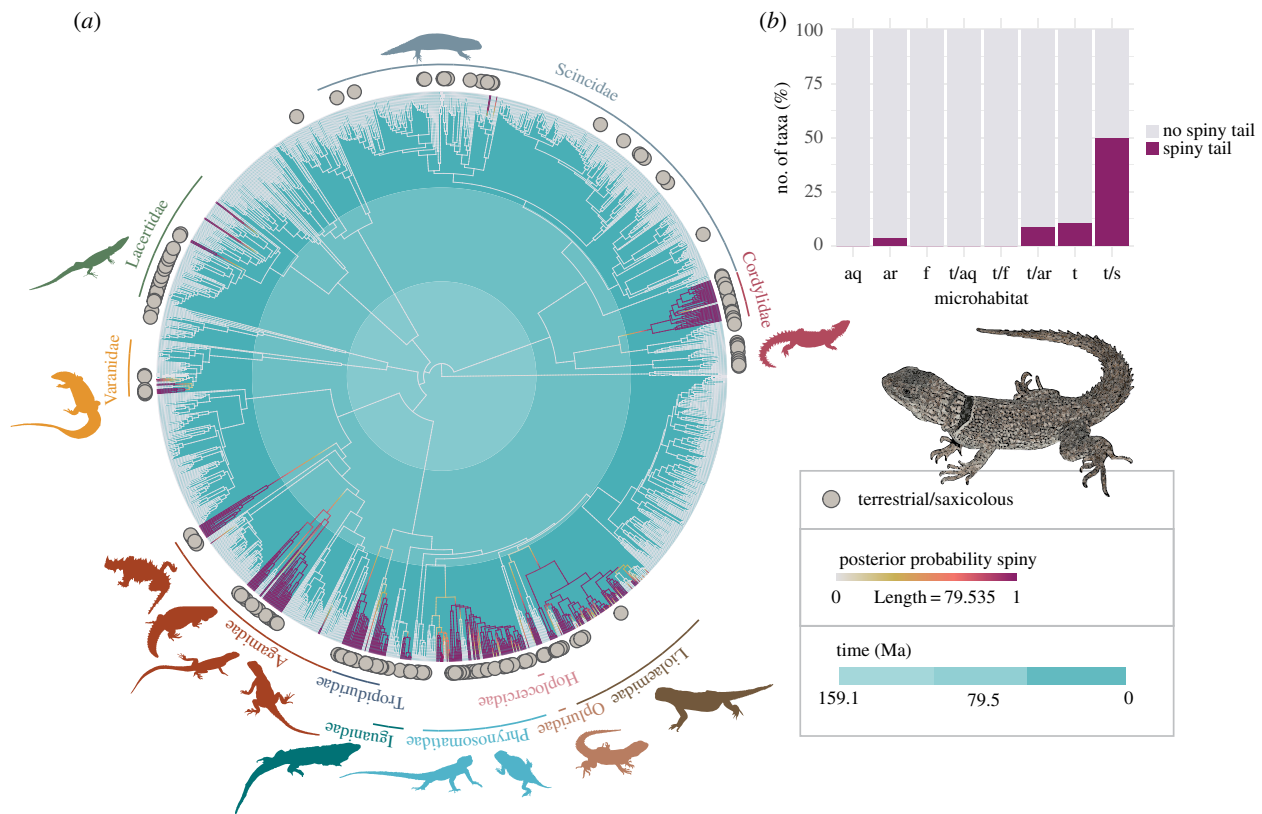


Figure 1. (a) Time-calibrated phylogeny of squamates showing posterior probabilities of the origin of spiny tails, from 1000 replicates of stochastic character mapping (SPINY dataset). The occupation of a terrestrial/saxicolous habitat is indicated by grey circles. Labelled families represent those containing spiny-tailed lizards. Geckos and snakes are omitted for better visualization. (b) Proportions of spiny-tailed squamates in different microhabitats. Abbreviations: aq, aquatic; ar, arboreal; f, fossorial; t/aq, terrestrial/aquatic; t/f, terrestrial/fossorial; t/ar, terrestrial/arboreal; t, terrestrial; t/s, terrestrial/saxicolous.

Table 1. Significance and log-likelihood values for different models of evolution between spiny tails and microhabitat in squamates. Asterisks indicate significance ($p < 0.05$) of Bonferroni-corrected p -values.

microhabitat	SPINY			SPINY STRICT		
	InL uncorrelated	InL correlated	corrected p -value	InL uncorrelated	InL correlated	corrected p -value
terrestrial	−1515.79	−1490.63	$9.45 \times 10^{-11*}$	−1411.39	−1407.63	0.19
terrestrial/saxicolous	−894.46	−838.91	$5.98 \times 10^{-24*}$	−790.05	−761.64	$3.68 \times 10^{-12*}$
aquatic	−479.28	−478.16	1	−374.88	−373.83	1
terrestrial/aquatic	−532.76	−529.88	0.45	−428.36	−428.18	1
arboreal	−996.15	−994.16	1	−891.74	−882.05	$4.94 \times 10^{-4*}$
fossorial	−605.22	−603.49	1	−500.81	−499.34	1
terrestrial/fossorial	−569.65	−569.30	1	−465.25	−464.90	1
terrestrial/arboreal	−943.17	−941.21	1	−838.77	−834.38	0.10

significantly more likely to have spiny tails compared to all other microhabitats across all datasets (see also figure 1b; electronic supplementary material, table S5).

(c) Body size and spiny tail evolution

Using phylogenetic logistic regression and phylogenetic ANOVA, we found no consistent differences in body size between spiny and non-spiny-tailed lizards (electronic supplementary material, tables S6, S8). Phylogenetic ANOVA testing showed a significant difference between body size in some pairwise microhabitat comparisons, with terrestrial/

aquatic species being significantly larger than fossorial species, when testing all squamates (in both the primary and STRICT dataset). When testing only lizards, aquatic species were significantly larger compared to species in all other microhabitats, while terrestrial/aquatic species were larger compared to terrestrial/fossorial species in both the primary and STRICT dataset (electronic supplementary material, table S7).

(d) Diversification rate analysis

Our state-dependent diversification rate analyses found that the best fitting model was a model of trait-dependent

diversification. By contrast, we found that a HiSSE null model fit best for the STRICT dataset, suggesting heterogeneity in diversification rates (in contrast to a BiSSE null model, which assumes that diversification rate is constant across the tree), and also indicating the absence of a hidden state in this dataset (electronic supplementary material, table S3). However, these results were not consistent when snakes were removed from the dataset (electronic supplementary material, table S3).

4. Discussion

Our analyses revealed that the evolution of spiny tails is significantly correlated with saxicolous microhabitats, and that when controlling for phylogenetic relatedness, saxicolous lizards are significantly more likely to have spiny tails than lizards associated with other microhabitat categories. These results put behavioural observations of spiny-tailed lizards (e.g. [15–17]) in a broader context, and we suggest that spiny tails may have the same antipredatory function in a variety of saxicolous species.

It is interesting to note that tail armour is still present in rock-dwelling species, even if selection acts against body armour. As shown for cordylid lizards, lighter body armour can be beneficial to increase escape speed [1] or to facilitate efficient thermoregulation in colder climates [7,8]. However, tail spines are present in all saxicolous cordylid genera, even if body armour is reduced [8]. This suggests that body and tail armour are subject to, and are the result of, differing selective pressures. Furthermore, several spiny-tailed lizards have lost the ability to shed their tails [30]. Given the high number of spiny-tailed squamates in saxicolous microhabitats (figure 1b), it seems plausible that the loss of tail shedding ability is advantageous for species that use their spiny tails to prevent extraction from crevices.

No consistent differences in body size or diversification rates of spiny-tailed versus non-spiny-tailed squamates were observed, in contrast to patterns observed in all amniotes [14]. However, we found significant correlations between spiny tails and other microhabitats in some of the datasets (i.e. terrestrial and arboreal microhabitats). Tail spines can be advantageous in preventing extraction from, e.g. tree hollows [13,31], thus potentially having a similar function as in saxicolous microhabitats. However, spiny tails can also be employed as weapons, e.g. via tail slashing in some terrestrial species [14,15], or to enlarge tail surface, such as in the gliding lacertid *Holaspis* [32]. Spines of the tail and body are also observed in slow moving ant-eating lizards like the agamid *Moloch* and the iguanian *Phrynosoma* [33,34]. Because of their diet, these species spend more time in open areas and have apparently evolved sharp spines as protection [33], independent of the usage of hollows or

crevices. The two main microhabitat categories in which no spiny-tailed species are present are fossorial/semi-fossorial and aquatic/semi-aquatic microhabitats. We assume that in the absence of other constraints, tail spines could be advantageous in these habitats for the same above-mentioned reasons as in other microhabitats. As such, their complete absence is likely due to ecological constraints related to locomotion in soil and water, respectively.

Despite the relative infrequency of tail spines among squamates, the trait seems highly labile (up to 38 origins in 11 different families), with spiny-tailed and non-spiny-tailed species often occurring in the same genus (figure 1a; see also [8] on the variation of body armour in cordylid lizards). While we found a high number of transitions between trait states, the D statistic indicated that closely related species are more likely to share the same trait state (negative observed D). Indeed, some families show a high number of spiny-tailed species while the trait is rare in others (figure 1). One major family in which spiny tails are completely lacking is Gekkonidae, possibly as a consequence of the general lack of osteoderms and hard keratinous structures in most species (see e.g. [35]). While some members of the genus *Strophurus* possess spiny structures on their tails, these are soft and involved in biochemical defence [36].

The evolution of spiny tails as both a defensive morphological trait and in a specific habitat type adds further evidence to the hypothesis that, in some cases, defensive traits might not evolve as a direct response to predators (see [8,37]. As suggested by Broeckhoven *et al.* [8], environmental factors may play a crucial role also in the evolution of defensive tail morphologies. Saxicolous lizards spend considerable amounts of time in rocky crevices for thermoregulation [38]. As such, traits associated with predator avoidance inside these crevices may be consequential to the adaptation to a saxicolous lifestyle. Our results support a coupled interaction between environment and predator–prey interactions as drivers in the evolution of defensive morphologies in reptiles.

Data accessibility. Data are available from the Dryad Digital Repository: <https://doi.org/10.5061/dryad.4qrf6q6j> [39].

Authors' contributions. T.R. conceived the study. T.R. and J.M. collected the trait data. T.R. and E.J.R. carried out the statistical analyses. T.R. drafted the manuscript with substantial intellectual contributions from E.J.R. and J.M. All authors agree to be held accountable for the content therein and approve the final version of the manuscript.

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