

Research



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Evolutionary biology

Parthenogenesis is self-destructive for scaled reptiles

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Parthenogenesis is rare in nature. With 39 described true parthenogens, scaled reptiles (Squamata) are the only vertebrates that evolved this reproductive strategy. Parthenogenesis is ecologically advantageous in the short term, but the young age and rarity of parthenogenetic species indicate it is less advantageous in the long term. This suggests parthenogenesis is self-destructive: it arises often but is lost due to increased extinction rates, high rates of reversal or both. However, this role of parthenogenesis as a self-destructive trait remains unknown. We used a phylogeny of Squamata (5388 species), tree metrics, null simulations and macroevolutionary scenarios of trait diversification to address the factors that best explain the rarity of parthenogenetic species. We show that parthenogenesis can be considered as self-destructive, with high extinction rates mainly responsible for its rarity in nature. Since these parthenogenetic species occur, this trait should be ecologically relevant in the short term.

1. Background

Asexual reproduction in vertebrates is rare. It occurs in squamates, fish, salamanders and frogs through gynogenesis, hybridogenesis, kleptogenesis and parthenogenesis [1]. While the former three mechanisms require male fertilization, in parthenogenesis, the embryo develops from a female gamete alone. Particularly, true/constitutive parthenogenesis (i.e. sperm-independent asexual reproduction) is even rarer: it occurs solely in scaled reptiles (order Squamata; e.g. [1–4]) from the successful hybridization between genetically distant species [1,5,6]. The explanation for the macroevolutionary rarity of parthenogenesis in vertebrates remains elusive [1,4,7]. We focus on parthenogenesis, although most aspects also apply to asexual vertebrates as we highlight below. Unless stated otherwise, we use ‘asexual’ for overall asexuality, ‘parthenogen’ for true/constitutive parthenogenesis and ‘species’ for each evolutionary unit in a phylogeny (i.e. evolutionary species concept [8]). Although the term ‘species’ has different meanings between reproductive modes, asexual species share some characteristics with sexual species (e.g. they evolve independently and each individual is more closely related to an individual of the same species than to individuals of a different species [9]).

The relatively young age and small number of parthenogenetic vertebrate species suggest that asexuality is evolutionarily disadvantageous in the long term [10]. It rather functions as a short-term successful ecological strategy [4,11] (reviewed in [1]). No ancient species-rich clade of asexual species is known to occur in nature; only distantly related species [4,6]. This can result from clones’ high extinction rates in the long term due to low recombination—Muller’s Ratchet [12]. The lack of DNA-repair meiotic mechanisms can also hinder asexual long-term viability [13] (however, asexual vertebrates can have

functional meiosis [14,15]). Finally, asexual species' low genetic diversity [1,5] could hinder their adaptability to changing environments [16]. However, if clones' formation is fast enough, neutral replacement could take place before their long-term disadvantages [17,18].

In the short term, asexuality can be ecologically successful. It can rapidly lead to population increases (i.e. no need for mating) and range expansions through the colonization of environments that are unsuitable for the parental species (i.e. geographic parthenogenesis) [1,5]. When parthenogenetic populations colonize new and species-poor environments, they expand their distribution of phenotypes and niche breadths (i.e. ecological release) [7]. Parthenogenetic lizards can even outcompete their sexual progenitors in some cases [19] and have greater aerobic activity at low temperatures [20].

When a trait arises often but increases extinction rates, leading to short-lived and phylogenetically scattered species, it is self-destructive [21]. Self-destructive traits are also labile—frequently gained and lost, particularly when the rate of reversal (i.e. loss of the trait) is high [21]. Examples include salt tolerance (increased extinction rates or high trait reversal) [22] and selfing (high trait reversal) [23] in plants and colour polymorphism in birds (increased extinction rates) [24] (but see [21]). Asexuality could be considered a self-destructive trait [21]; the phylogenetic 'instability' suggests either increased extinction rates, trait lability or both. However, studies with invertebrates show no negative impact of asexuality on diversification rates [25,26]. Alternatively, the likelihood for asexual formation through hybridization could explain this 'instability' [5,27]. Successful hybridization relies on a range of overlap between parental species, while maintaining enough phylogenetic distance and genetic compatibility [27–30]. The role of asexuality as a self-destructive trait remains untested at the macroevolutionary level for vertebrates.

Squamates are a suitable system for studying the macroevolutionary dynamics of asexuality while focusing on parthenogenesis. There are 39 parthenogenetic squamates reported so far (e.g. [7]). We used four tree metrics, null simulations and alternative scenarios of trait evolution to test parthenogenesis as a self-destructive trait in Squamata. First, we addressed if parthenogenetic species are younger than sexual species. Parthenogenetic species should be younger (i) if they arise frequently in nature but are relatively short lived (higher extinction rates) and (ii) given they generally originate from hybridization [1]. Second, we compared if the number of parthenogenetic species per origin of parthenogenesis is lower than expected. We expect each origin of parthenogenesis to give rise to fewer than expected parthenogenetic species. Not only will parthenogenesis formation depend largely on the amount of range overlap and genetic diversity between hybridizing species [1]; in a scenario of self-destruction, parthenogenetic species would frequently go extinct before possibly radiating. Together, these would hinder the accumulation of parthenogenetic species per origin of parthenogenesis. Third, we tested if parthenogenetic species are clustered or scattered. In a scenario of trait self-destruction, parthenogenetic species should be scattered throughout the phylogeny. Finally, we inferred the parameters responsible for the unstable macroevolutionary pattern of parthenogenesis under different scenarios. We expect that increased extinction rates will best explain this pattern given the long-term limitations of parthenogenesis.

Table 1. Estimates of four tree metrics on the consensus tree ($n = 5388$). Significant values ($p < 0.05/p > 0.95$ for TARS, NoTO and SSCD; FPD > 0.5) are boldfaced.

metric	consensus tree
tip age rank sum (P_{TARS})	32576.0 (<0.001)
number of tips per origin (P_{NoTO})	1.278 (0.278)
sum of sister clade differences (P_{SSCD})	35.376 (0.103)
Fritz & Purvis D statistic	0.401

2. Methods

(a) Species data and phylogenies

We identified 39 parthenogenetic species of Squamata from the literature (see electronic supplementary material, table S1). We used only species included in [31].

We used the posterior distribution of 10 000 phylogenies of Squamata with 9754 species each [32]. We pruned all trees using ape v. 5.3 in R [33] to the species with molecular data in [32]. The final set of phylogenies included 5388 species. We calculated the 50% majority-rule consensus tree in MrBayes v. 3.2 [34]. The final tree included 23 out of 39 parthenogens (electronic supplementary material, table S1). We examined the effects of (i) phylogenetic uncertainty using an alternative tree and (ii) sampling bias by randomly allocating the state 'parthenogen' within each genus where the trait is known to occur (electronic supplementary material, text S1 and S2).

(b) Phylogenetic metrics

We calculated four tree metrics for the consensus tree: tip age rank sum (TARS), number of tips per origin (NoTO), sum of sister clade differences (SSCD) and Fritz & Purvis D statistic (FPD) [21,35]. We used phylometrics v. 0.01 in R [36] and tested for significance using the Wilcoxon rank-sum test for TARS, 1000 traits simulated under Brownian motion (BM) for NoTO and SSCD, and 1000 traits simulated under BM and 1000 random traits for FPD [21]. When $P_{\text{TARS}} < 0.05 / > 0.95$, parthenogenetic species have significantly shorter/longer tip lengths than sexual species. When $P_{\text{NoTO}} < 0.05 / > 0.95$, each inferred origin of parthenogenesis (which is placed at the node for each independent parthenogenetic species or clade of parthenogenetic species) gives rise to fewer/more species than expected under a stochastic process. When $P_{\text{SSCD}} < 0.05 / > 0.95$, parthenogenetic species are more scattered/clustered than expected under a stochastic process. When absolute values of FPD are closer to 1, parthenogenetic species are randomly distributed throughout the phylogeny, while values closer to 0 indicate that the trait evolves as expected under BM.

(c) Macroevolutionary models

We simulated different scenarios of trait evolution to test the parameters responsible for the macroevolutionary dynamics of parthenogenesis in squamates. The parameters include speciation rate for sexual (λ_0) and parthenogenetic species (λ_1), extinction rate for sexual (μ_0) and parthenogenetic species (μ_1), and rates of gain (q_{01}) or reversal (q_{10}). The initial values were 0.1, 0.1, 0.03, 0.03, 0.01 and 0.01 (in units: per million years), respectively [21]. Since the method uses likelihood estimation, we repeated the analysis with these values both multiplied and divided by 5.

We simulated nine scenarios for each set of initial parameters under different constraints: no effect of parthenogenesis on speciation rates ($\lambda_0 = \lambda_1$) and/or extinction rates ($\mu_0 = \mu_1$), equal

Table 2. Parameter maximum-likelihood estimates under macroevolutionary scenarios of trait evolution (*a–i*) using the starting parameters for the consensus tree ($n = 5388$). Parameters include speciation rates for sexual/parthenogenetic species (λ_0/λ_1), extinction rates for sexual/parthenogenetic species (μ_0/μ_1) and rates of gain/reversal of parthenogenesis (q_{01}/q_{10}). Rejected models are boldfaced (figure 1).

macroevolutionary scenario	λ_0	λ_1	μ_0	μ_1	q_{01}	q_{10}
(a) no constraints	0.048	0.27	2.0×10^{-8}	2.4×10^{-6}	1.8×10^{-3}	0.30
(b) $\lambda_0 = \lambda_1, \mu_0 = \mu_1, q_{01} = q_{10}$	0.059	0.059	2.3×10^{-5}	2.3×10^{-5}	2.1×10^{-4}	2.1×10^{-4}
(c) $\lambda_0 = \lambda_1, \mu_0 = \mu_1$	0.059	0.059	6.2×10^{-7}	6.2×10^{-7}	4.2×10^{-4}	0.13
(d) $\lambda_0 = \lambda_1, q_{01} = q_{10}$	0.059	0.059	3.3×10^{-5}	0.27	8.6×10^{-4}	8.6×10^{-4}
(e) $\mu_0 = \mu_1, q_{01} = q_{10}$	0.059	0.085	1.8×10^{-9}	1.8×10^{-9}	2.1×10^{-4}	2.1×10^{-4}
(f) $\lambda_0 = \lambda_1$	0.059	0.059	2.7×10^{-6}	2.5×10^{-5}	3.9×10^{-4}	0.13
(g) $\mu_0 = \mu_1$	0.048	0.27	2.9×10^{-6}	2.9×10^{-6}	1.8×10^{-3}	0.30
(h) $q_{01} = q_{10}$	0.059	0.24	3.4×10^{-7}	0.49	1.1×10^{-3}	1.1×10^{-3}
(i) $q_{10} = 0$	0.059	0.13	1.6×10^{-7}	0.46	1.2×10^{-3}	0

transition rates ($q_{01} = q_{10}$) or no reversals ($q_{10} = 0$). The scenarios include (a) no constraints—parameters can be different between sexual and parthenogenetic species; (b) $\lambda_0 = \lambda_1, \mu_0 = \mu_1$ and $q_{01} = q_{10}$; (c) $\lambda_0 = \lambda_1$ and $\mu_0 = \mu_1$; (d) $\lambda_0 = \lambda_1$ and $q_{01} = q_{10}$; (e) $\mu_0 = \mu_1$ and $q_{01} = q_{10}$; (f) $\lambda_0 = \lambda_1$; (g) $\mu_0 = \mu_1$; (h) $q_{01} = q_{10}$ and (i) $q_{10} = 0$. We fit each model using diversitree v. 0.9-13 in R (table 2; electronic supplementary material, table S3 and S4) [37].

To obtain a null distribution of tree metrics for the macroevolutionary scenarios, we used the parameters estimated in models *a–i* to simulate 100 trees with 5388 species. We then estimated the tree metrics in the alternative scenarios. *p*-Values indicate the proportion of simulated metric values that are lower than or equal to the observed metric values. Significance was considered if $p \leq 0.01/p \geq 0.99$ after a Bonferroni correction [35]. Overall, we were interested in the relative role of each parameter and not in the specific fitted values of the rates. We tested for false discovery rates (model *b*) and power (models *a, c–i*) as the proportion of simulated metric values with $p \leq 0.05$ for $P_{\text{TARS}}, P_{\text{NoTO}}$ and P_{SSCD} , or $p > 0.5$ for P_{FPD} (electronic supplementary material, table S11–S13) [21].

3. Results

Parthenogenetic species are significantly younger than sexual species ($P_{\text{TARS}} < 0.001$; table 1). The number of species that originate from parthenogenetic ancestors does not differ from those that originate from a trait evolving under BM ($P_{\text{NoTO}} = 0.278$). Species are not more scattered across the phylogeny than expected under BM ($P_{\text{SSCD}} = 0.103$) nor more randomly distributed (FPD = 0.401). Results were consistent using an alternative phylogeny and to the impact of missing taxa (electronic supplementary material, table S2).

Models *c, d, f, h* and *i* identify parthenogenesis as self-destructive either by higher extinction rates compared to speciation (*d, h, i*) or high rates of reversal (*c, f*) (table 2). These models were not rejected (figure 1) and parameters suggest that parthenogenesis in squamates cannot be distinguished from a model where this state is frequently lost due to high extinction rates (*d, h, i*) or high rates of reversal (*c, f*). Models *a* and *g* also have high rates of reversal, but the speciation rates are higher relative to extinction. Model *e* reflects a trait that increases/decreases speciation. Results were consistent using different initial parameters (electronic supplementary material, table S3 and S4) and alternative approaches (electronic supplementary material, text S1 and

S2). We found low false discovery rates and high power to detect significant effects for each macroevolutionary scenario (electronic supplementary material, table S11–S13).

4. Discussion

Here, we show that parthenogenesis in squamates can be considered a macroevolutionary self-destructive trait. Parthenogenetic species are significantly younger than sexual species. However, each origin of parthenogenesis does not give rise to fewer than expected parthenogenetic species. This could reflect some genera as *Darevskia* or *Aspidoscelis* that concentrate almost half of the described parthenogenetic squamates (approx. 46%). Subsequent backcrosses could explain how each origin of parthenogenesis could give rise to more than one parthenogenetic species [5,38]. In fact, the uneven incidence of true parthenogens could explain that parthenogenesis is not as scattered in the phylogeny as expected. Only one species of Serpentes (i.e. *Indotyphlops braminus*) has been described as true parthenogenetic (figure 2). This suggests a higher tendency for lizards to produce parthenogenetic hybrids or biases towards the most studied clades [39]. Null simulations should benefit from increased numbers of described parthenogenetic species and further motivate identifying asexual species in nature.

Results from the macroevolutionary scenarios also support parthenogenesis as self-destructive. At first glance, results suggest that this trait increases extinction rates or rates of reversal. However, once asexuality is achieved, reversals to sexual reproduction would be very difficult [6,40] (but see [41]), particularly if the genes responsible for sexual traits (e.g. spermatogenesis and meiosis) degenerate [1,6]. This suggests that trait lability is not responsible for the ‘unstable’ pattern of parthenogenesis. We do not reject model *i* that identifies higher extinction rates in relation to speciation and null rates of reversal (figure 1). Thus, although high rates of reversal can also explain similar scenarios of trait evolution, the difficulty associated with the reversal from asexuality indicates this should not be the case for parthenogenesis. Ultimately, parthenogenesis influences extinction rates (model *d*), even when coupled with a smaller effect on speciation rates (models *h, i*; table 2). While clonal diversity seems related to the balance between speciation and extinction [42],

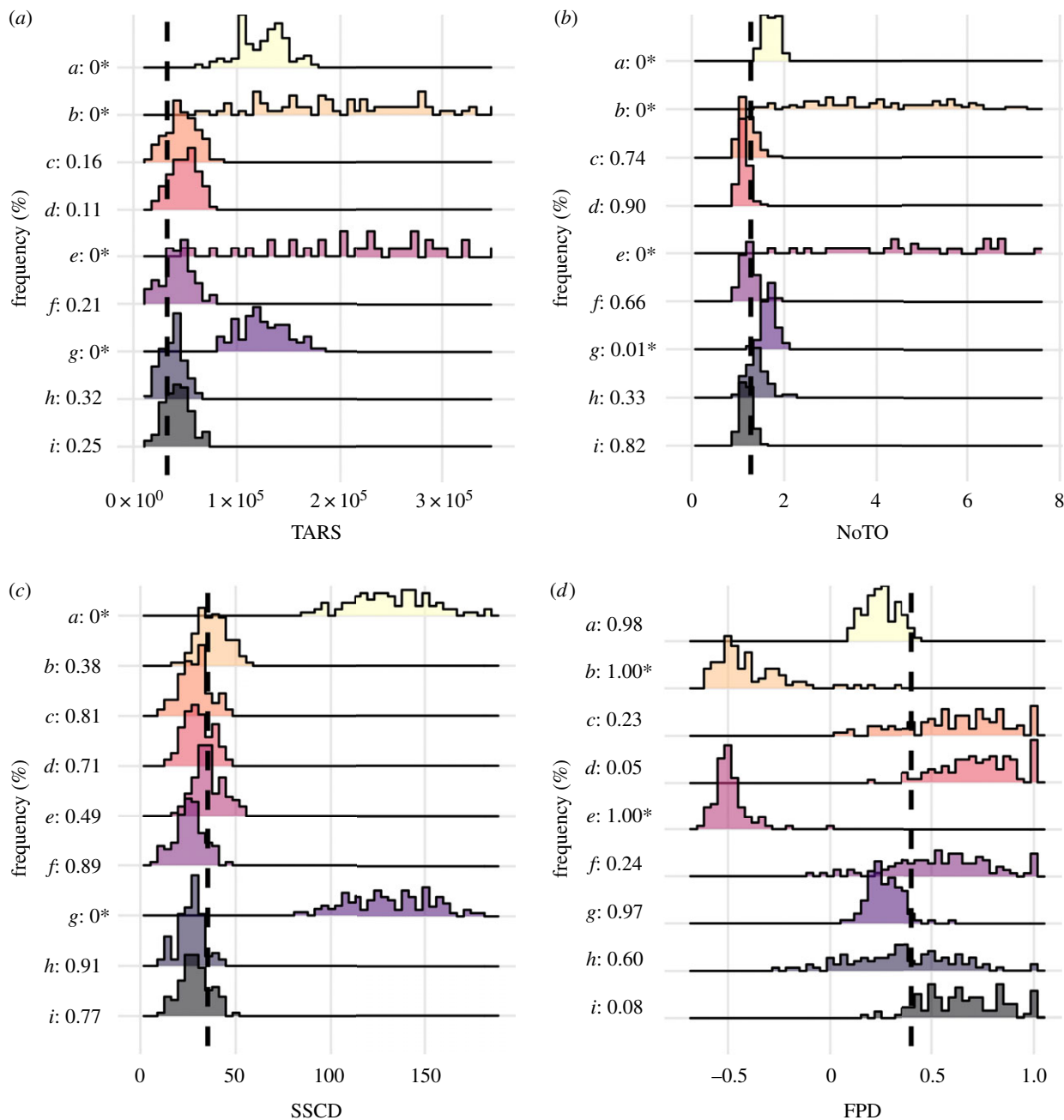


Figure 1. The null distribution of four tree metrics for distinct macroevolutionary scenarios (*a–i*; coloured histograms) using the starting parameters for the consensus tree ($n = 5388$). Dashed lines represent the observed metric value. Frequency (%) represents the proportion of simulated metric values that are lower than or equal to the observed. Significant values ($p \leq 0.01/p \geq 0.99$) are marked with an asterisk (*).

estimated extinction rates as high as 10^{-1} , exceeding speciation rates (table 2), suggest that parthenogenetic species would go extinct before possibly giving rise to additional parthenogenetic species. Note, however, that these speciation events are different from those in sexual species as they involve subsequent backcrosses [5,38]. In practice, new parthenogenetic species would reflect new evolutionary units in the phylogeny. Whenever speciation rates for parthenogenetic species approaches extinction, the model was rejected (model *h*; electronic supplementary material, table S4).

The low frequency of hybridization [5,27] does not seem to explain the macroevolutionary pattern we observe in squamates; we reject model *e* that indicates an effect of parthenogenesis solely on speciation (table 2). Besides, in models *h* and *i* (not rejected) speciation rates were higher for parthenogenetic species. This contradicts the idea of reduced origination events for parthenogenetic species compared to sexual species.

Also, assuming that each parthenogenetic species originates only once underestimates the origination rate for asexuality. Genotyping of *Darevskia armeniaca*, for example, suggests multiple interspecific origins between *D. valentini* and *D. mixta* [43] (but see [5]). Nevertheless, in models where the speciation rates were allowed to vary (models *a*, *e*, *g–i*), speciation rates for parthenogenetic species were always higher than speciation rates for sexual species. Models *a*, *e* and *g* were rejected. Models *h* and *i*—indicative of parthenogenesis self-destruction—were not rejected. Underestimation of parthenogens origination rates should have little impact on the results.

Neutral replacement of parthenogenetic species is an alternative explanation to the relative younger age of parthenogens. Before becoming extinct due to inherent ecological hindrances, parthenogenetic species could be younger from the neutral replacement of existing clones [18,40,44]. Authors further argue that it is difficult to distinguish neutral

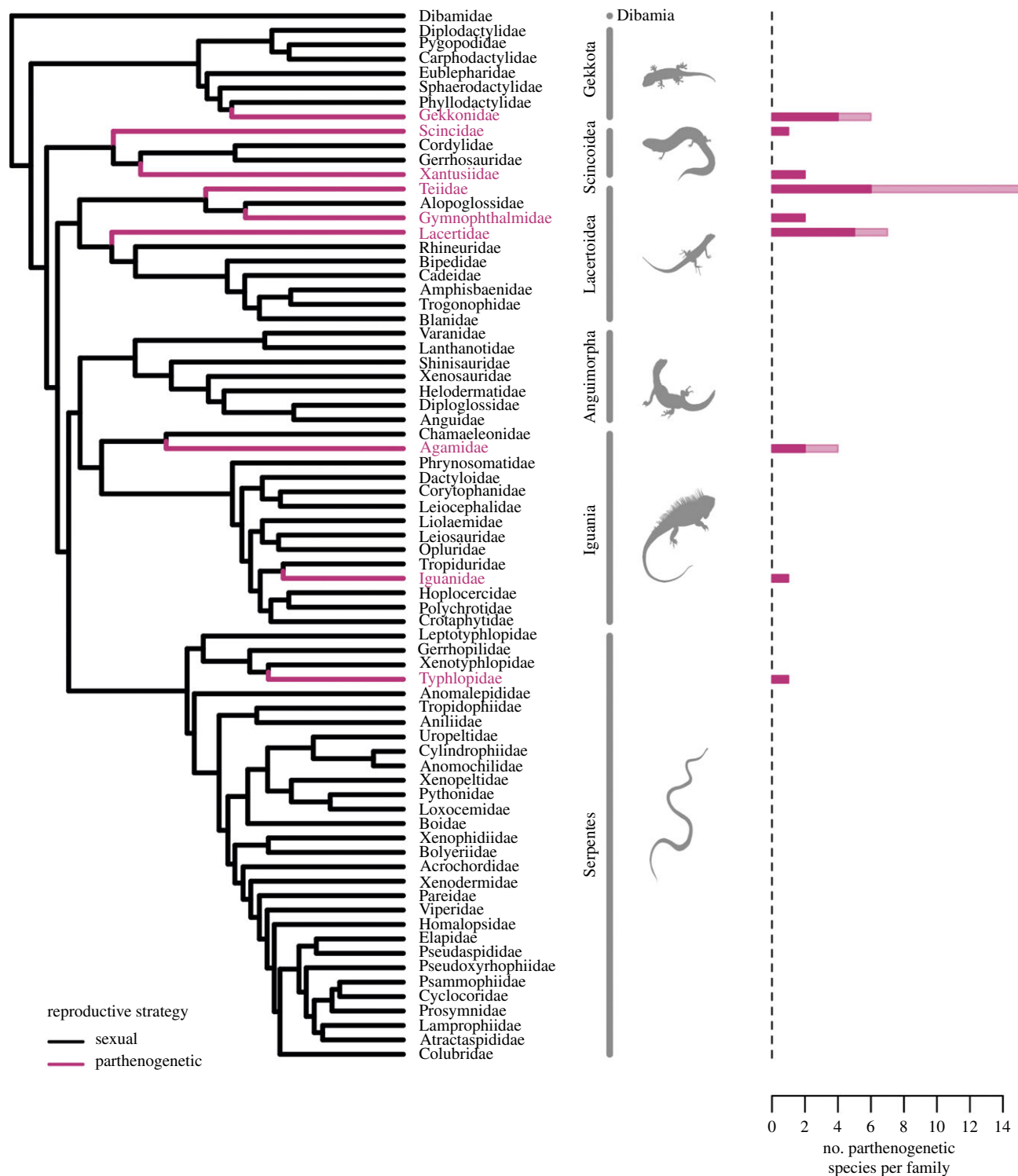


Figure 2. Incidence of true/constitutive parthenogenesis in Squamata. The tree is drawn at the family level, but all analyses were performed at the species level ($n = 5388$). Coloured edges/tip labels (solid purple) represent families that include parthenogenetic species. The bar plot represents the number of parthenogenetic species per family included (solid purple) and the number of described parthenogenetic species per family (transparent purple). Vertical grey lines and silhouettes indicate the seven major clades.

replacement from increased extinction rates. In a scenario of clones' high turnover for each parthenogenetic species, we would expect the same outcome in our macroevolutionary models focused on the TARS metric (i.e. parthenogenetic species are younger than sexual species). Also, we would expect higher clone turnover to influence the number of parthenogenetic species per origin of parthenogenesis and the parthenogenetic species clustering. Specifically, if clones' neutral turnover continuously replaces older clones, this prevents them from ageing. Subsequently, this would decrease the

chance for new parthenogenetic species to establish and form species clusters. Importantly, authors focus on the within-species level to distinguish processes occurring at the micro from the macroevolutionary level. Here we use a combination of macroevolutionary metrics that focus on interspecific age comparisons, origination events, species clustering and simulations of alternative scenarios of trait evolution.

Asexuality is not a simple phenomenon. We used parthenogenetic species alone and simplified some aspects of hybridizing species. We considered parthenogens at the species

level (but see [9]) and we did not account for backcrossing [5] or the complex reticulate topology in some genera [38]. By simplifying the models, we focused on the macroevolutionary dynamics of parthenogenesis in squamates rather than the microevolutionary mechanisms underlying parthenogenesis. Our results suggest that parthenogenesis could be self-destructive in the long term, possibly explaining the 'unstable' pattern observed for parthenogenesis in Squamata.

Data accessibility. All data and code are available from the Dryad Digital Repository: <https://doi.org/10.5061/dryad.sqv9s4n3c> [45].

Authors' contributions. M.O.M. and D.R. conceived the main ideas; M.O.M. performed the analysis; all authors contributed to the

analysis of the results and the writing of the paper; all authors gave final approval for publication and agree to be held accountable for the work performed therein.

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