



SLOW AND FAST EVOLUTIONARY RATES IN THE HISTORY OF LEPIDOSAURS

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Abstract: Biodiversity today is uneven, with equally ancient sister groups containing few or many species. It has often been assumed that high biodiversity indicates fast evolution, and yet in a classic work in 1944 George Simpson suggested that fast evolution might generate instability and extinction, and that slow evolution led to high biodiversity. Here we show that evolutionary rates can vary substantially through the history of a clade and find evidence for Simpson's claim. In a comparative phylogenetic study deploying Bayesian methods, we find that Squamata, comprising today over 10 000 species of lizards and snakes, showed slow rates of evolution in the first two-

thirds of their history, whereas their sister clade, Rhynchocephalia, comprising just one living species, showed high rates of evolution in the past. Slow and steady won the race for the Mesozoic squamates, and the high-rate boom and bust existence of rhynchocephalians at that time leaves them with a single survivor. We need to explore other cases where fast evolution can lead to short-term high diversification, but in the end long-term low biodiversity.

Key words: Lepidosauria, Rhynchocephalia, Squamata, rates of evolution, body size evolution.

IN the evolution of biodiversity, many large clades appear to have arisen through fast evolution whereas smaller groups experienced slow evolution (Darwin 1859; Simpson 1944). Phenotypic evolvability, or greater evolutionary versatility, should promote speciation and make clades persistent on macroevolutionary timescales (Vermeij 1973; Rabosky *et al.* 2013). In a classic work on evolution, Simpson (1944) countered this idea, suggesting that lineages with high phenotypic evolutionary rates were likely to be more prone to extinction, and successful groups perhaps evolved slowly. In particular, Simpson (1944) argued that high rates of evolution were unlikely to be sustained for long because the fast-evolving clade might be so volatile as to go extinct or would switch to a slower evolutionary rate.

Simpson (1944) linked his ideas about rates of evolution to the concept of adaptive radiations and stressed how clades could expand fast initially in terms of species richness, which is related to the 'early burst' model of clade evolution. In exploring these assumptions about adaptive radiation, Harmon *et al.* (2010) found that, while early bursts were often documented in smaller clades increasing trait values rapidly within lakes or other restricted settings, deep-time studies at global scale rarely showed such early burst models. Harmon *et al.* (2010)

found that large-scale trait expansions in clades rarely matched an early burst model, but more commonly a selective peak model (random walk with a single stationary peak to which trait values returned), or even a random walk model.

Palaeontologists, on the other hand, have long identified 'early burst' models as the best explanations for many clade expansions, and in a variety of contexts. For example, Sepkoski (1984) argued that his major marine 'faunas', the 'Cambrian', 'Palaeozoic' and 'Modern', diversified according to a logistic pattern, with an initial slow phase, then a rapid rise in diversity, followed by a density-determined asymptote (Foote 2000). Westoll (1949) showed how the rate of trait acquisition in lungfish followed an exponential curve, with a very high rate of character acquisition initially, and stasis since the Permian and Triassic. In studies of trilobites, crocodylians, dinosaurs, and many other groups, early burst patterns of trait diversification have been identified (e.g. Benson *et al.* 2014; Godoy *et al.* 2019; Paterson *et al.* 2019). On the other hand, Clarke *et al.* (2016) showed heterogeneous patterns of evolution in bony fishes, with teleosts showing initially low phenotypic evolutionary rates, whereas holosteans had fast rates, unexpected based on the current diversity of each clade and assumptions of fast trait

evolution in teleosts. Here we explore an analogous case in Lepidosauria.

The reptilian Superorder Lepidosauria includes the Rhynchocephalia (tuataras) and the Squamata (lizards, snakes and amphisbaenians). The 10 000 species of living squamates are distributed worldwide, and their morphologies and ecologies vary from tiny chameleons on Madagascar which are the size of a thumbnail to 10-m-long anacondas and similarly huge extinct marine mosasaurs (Jones *et al.* 2013; Simões *et al.* 2018). Squamate modes of life range through aquatic, terrestrial and aerial lifestyles, feeding on seaweed, plants, insects and mammal prey. By contrast, the Rhynchocephalia are represented today by the single species *Sphenodon punctatus*, which is geographically restricted to the islands of New Zealand (Jones *et al.* 2013).

The extant diversity of Lepidosauria represents just a snapshot of their long evolutionary history. Lepidosaur origins have been dated to the Early or Middle Triassic (Jones *et al.* 2013), while others propose a middle Permian origin (Simões *et al.* 2018), based on projected dates from Middle Triassic squamate fossils. During early lepidosaur evolution, the Rhynchocephalia was the more successful and morphologically diverse group and earliest squamates were much less diverse (Evans & Jones 2010). During the Cretaceous there was a turnover in lepidosaurian diversity; rhynchocephalians declined, but squamates underwent a massive radiation including both morphological and phylogenetic expansion (Evans & Jones 2010; Cleary *et al.* 2018; Herrera-Flores *et al.* 2021a). Most of the major squamate clades diversified during the Cretaceous and persisted after the Cretaceous–Palaeogene (K–Pg) mass extinction event 66 million years ago (Ma). However, some successful subgroups became extinct, such as the polyglyphanodontian lizards and predatory marine mosasaurs. During the Cenozoic, squamates continued to be important components of terrestrial ecosystems but rhynchocephalians were reduced to some relict species.

Here, we present a large-scale macroevolutionary analysis of rates of morphological evolution in early lepidosaurs using Bayesian phylogenetic comparative methods. We examine rate heterogeneity of body size evolution, a key trait associated with morphology, ecology and physiology, in Mesozoic and early Palaeogene lepidosaurs. We test the hypothesis that squamates show rapid evolutionary rates compared to rhynchocephalians, a hypothesis that might be assumed based on their present species richnesses (10 000 species vs 1 species). Our results demonstrate that the early evolution of lepidosaurs was characterized by heterogeneous rates of body size evolution and, unexpectedly, rhynchocephalians showed significantly higher rates than squamates during the Mesozoic.

METHOD

Lepidosaur phylogeny

An informal supertree of Mesozoic and early Palaeogene lepidosaurs was constructed by combining several recent phylogenies for rhynchocephalians and squamates. This was necessary because there have been no published phylogenies of all lepidosaurs, and because there are several current but conflicting phylogenies of squamates. We assembled the supertree in Mesquite (Maddison & Maddison 2002). For rhynchocephalians we used the maximum parsimony 50% majority rule consensus tree of Herrera-Flores *et al.* (2018, fig. 3). For early squamates (amphisbaenians, lizards, snakes and mosasaurs) we built a standardized supertree according to the latest consensus and by using as reference: the maximum parsimony strict consensus tree of Conrad (2008, fig. 54); the maximum parsimony strict consensus tree including only ingroup fossils of Gauthier *et al.* (2012, fig. 6); Adams consensus tree of Longrich *et al.* (2012, fig. 2); strict consensus tree of Caldwell *et al.* (2015, fig. 4b); maximum parsimony strict consensus tree of Martill *et al.* (2015, fig. 5); strict consensus tree of Longrich *et al.* (2015, fig. 5); maximum likelihood tree of Simões *et al.* (2017, fig. 1D); and maximum parsimony strict consensus tree of Rio & Mannion (2017, fig. 10B).

After the assembly of the backbone supertree, additional taxa were included by hand because some had never been included in cladistic analyses before, or their positions conflict between different topologies. We inserted these taxa by reviewing the original descriptions of some poorly known species and their possible phylogenetic affinities (full details in Herrera-Flores *et al.* 2021b).

In the case of squamates, we built a standardized supertree according to the latest consensus, but in order to avoid biasing the study to a single topology of the position of squamate higher clades (e.g. Mosasauria + snakes), and to account for phylogenetic uncertainty, we produced three supertree frameworks, with different topologies for squamate higher clades, based on the contrasting topologies of Conrad (2008), Gauthier *et al.* (2012) and Simões *et al.* (2018). For each supertree we generated a set of 100 trees with polytomies randomly resolved.

Phylogenetic time-scaling

Taxa were dated at geological stage and substage level, where possible. Age ranges were based on the most recent information available for each taxon. Absolute ages for geological stages were based on the 2019/05 version of the International Chronostratigraphic Chart (Cohen *et al.*

2013). We time-scaled the trees using the R implementation (R Core Team 2013; v.3.6.0) of the whole tree extended Hedman algorithm (Hedman 2010; Lloyd *et al.* 2016) to produce 100 time-scaled trees for each topology. We used the ‘conservative approach’ (Hedman 2010), which ignores taxa that are younger than the preceding outgroup and set the absolute maximum bound t_0 conservatively to the base of the Cambrian (542 Ma) following Lloyd *et al.* (2016).

We used the last appearance dates (LADs) of *Ichthyostega stensioi* (363.3 Ma), *Ymeria denticulata* (358.9 Ma), *Tulerpeton curtum* (358.9 Ma), *Ossirarus kierani* (350.8 Ma), *Casineria kiddi* (336.2 Ma), *Palaeomolgophis scoticus* (336.2 Ma), *Hylonomus lyelli* (315.2 Ma), *Anthracodromeus longipes* (307 Ma), *Petrolacosaurus kansensis* (303.7 Ma), *Orovenator mayorum* (286.8 Ma), *Lanthanolanian ivakhnenkoi* (265.1 Ma), *Eunotosaurus africanus* (259.1 Ma), *Weigeltisaurus jaekeli* (256.6 Ma), *Paliguana whitei* (251.2 Ma) and *Sophineta cracoviensis* (247.2 Ma) as outgroup ages. Resolution was set to 10 000.

To account for uncertainty in dating we randomly sampled the tip age of each lepidosaur species from a uniform distribution bounded by its first (FADs) and last appearance dates (LADs). The current R implementation of the Hedman algorithm (Lloyd *et al.* 2016) does not allow trees that are not fully bifurcating to be scaled. Therefore, to visualize the results on a consensus tree including polytomies and not for the analysis itself, we generated an additional time-scaled tree for each topology using the minimum branch length (MBL) method with a minimum branch length of 1 myr (Laurin 2004) as implemented in the timePaleoPhy function of the R package paleotree v.3.3.0 (Bapst 2012).

To test the impact of different time-scaling methods on our results we also used the fossilized birth–death (FBD) tip-dating approach (Stadler 2010; Heath *et al.* 2014; Zhang *et al.* 2016) as implemented in MrBayes v.3.2.7a (Ronquist & Huelsenbeck 2003; Ronquist *et al.* 2012). Topological constraints were based on the generated supertree topologies and an ‘empty’ morphological matrix was generated using the createMrBayesTipDatingNexus function of paleotree (Bapst 2012).

We identified and resolved two serious issues with the implementation of FBD runs in MrBayes. First, we found that MrBayes ignores topological constraints at the root, if the root node is fully resolved, so we added two outgroup taxa, the lepidosauromorphs *Sophineta cracoviensis* (249.2–247.2 Ma) and *Paliguana whitei* (251.9–251.2 Ma) to a polytomy at the root including the clade Lepidosauria. Tip age calibrations were defined as uniform priors bounded by the FADs and LADs of the tips. Similar to the approach of Godoy *et al.* (2019) and Button & Zanno (2020), we placed a uniform prior on the root of the tree bounded by the FAD of the potentially oldest

lepidosauromorph *Weigeltisaurus jaekeli* (259.1 Ma) (see Motani *et al.* 2015; Scheyer *et al.* 2017; but see also Pritchard & Sues 2019) and the FAD of the oldest tip on the tree (*Paliguana whitei*: 251.9 Ma). *Marmoretta oxoniensis* was used as the anchor taxon to place the time-scaled trees in absolute time.

We also found that for certain datasets, the current implementation of the FBD tip-dating approach in MrBayes v.3.2.7a ignores the tip age calibrations if no extant taxa are included (AE pers. obs. 2021). To avoid this problem, we subtracted the LAD of the youngest tip from the FADs and LADs of all tips, essentially moving the youngest tip to the present day. The root prior was modified accordingly. This approach also helped in improving convergence (see also Bapst *et al.* 2016).

Otherwise, we used the default FBD and clock priors provided by createMrBayesTipDatingNexus: fossilization rate = beta (1, 1); speciation rate = uniform (0, 10); extinction rate = beta (1, 1); sampling strategy = random; sampling probability = 1; clock rate = normal (0.0025, 0.1); clock variance = igr; igr variance = uniform (0.0001, 200) (following Matzke & Wright 2016). The analysis was run four times, using six chains per run, for 400 000 000 generations and sampling every 4000. Convergence was assessed using Tracer v.1.7.1 (Rambaut *et al.* 2018) with the effective sample size (ESS) of all parameters exceeding 200. The obtainDatedPosteriorTreesMrB function of paleotree was subsequently used to obtain a sample of 100 time-scaled trees from the posterior, employing a burn-in of 20%. We then added the (original) LAD of the youngest tip to the root.time element of the imported time-scaled trees and removed the outgroup taxa *Sophineta cracoviensis* and *Paliguana whitei* for the following analyses. For visualization purposes only we again generated additional MBL consensus trees (1 myr) for each topology.

Proxy for body size

Body size is a widely used trait in macroevolutionary studies (e.g. Venditti *et al.* 2011; Baker *et al.* 2015; Benson *et al.* 2018), because it influences a broad range of physiological and ecological traits. Ideally, we should use total body length or snout–vent length as a metric of size, as in studies of living squamates, but the fossil data are insufficient, and most Mesozoic squamate fossils lack postcranial remains (Herrera-Flores *et al.* 2021a). Therefore, we could not use femur length or any other postcranial proxy for body size but focused on skull length. Of various metrics for skull length, we selected mandible length because fossil lizard mandibles are most frequently complete and undistorted (Evans & Jones 2010; Cleary *et al.* 2018; Herrera-Flores *et al.* 2021a). A database with

167 lower jaw lengths was compiled for taxa with complete jaws (see Herrera-Flores *et al.* 2021b). Lower jaw measurements were taken from the largest specimens available from the literature, measured from photographs or directly taken from specimens reviewed by the authors. All size measurements were \log_{10} -transformed before analysis.

Evolutionary rates

We explored rate heterogeneity of body size evolution, a key trait associated with morphology, ecology and physiology (Stanley 1973; Schmidt-Nielsen 1984; Feldman *et al.* 2016) in Mesozoic and early Palaeogene Lepidosauria. We employed BayesTraits v.2.0.2 (Venditti *et al.* 2011) to estimate the variable rates models of body size evolution. BayesTraits uses a reversible jump Markov Chain Monte Carlo algorithm (rjMCMC) to detect shifts in the rate of evolution of a continuous trait across a phylogenetic tree. The tree branch lengths are optimized to conform to a Brownian motion model of evolution by rescaling the lengths of branches whose inferred variance of trait evolution deviates from that expected of a homogeneous Brownian motion model. The calculated scalars indicate the amount of acceleration or deceleration relative to the background rate on the branch of interest (Baker *et al.* 2016). We ran variable rates independent contrast models using the MCMC method with default priors for each time-scaled tree. Each tree was run for 120 000 000 iterations and parameters were sampled every 10 000 iterations; 20 000 000 iterations were discarded as burn-in. We calculated the marginal likelihood of the models using the stepping-stone sampler (Xie *et al.* 2011) implemented in BayesTraits. We sampled 1000 stones and used 100 000 iterations per stone. Convergence was assessed using the R package CODA v.0.19-2 (Plummer *et al.* 2006). The smallest effective sample size (ESS) value across all 600 trees was >489. We used the variable rates post processor (Baker *et al.* 2016) to extract the final parameters results. Models were compared using a Bayes factor (BF) test.

Rates results were summarized by calculating a consensus tree for all time-scaled trees where the branch lengths had been replaced with the mean rate scalars calculated by BayesTraits. The consensus tree was computed using the R package phytools v.0.6-99 (Revell 2012). We calculated the mean branch lengths for each set of trees, ignoring edges that were not present in all trees of a set. We then plotted the (rescaled) branch lengths of the consensus tree onto the MBL tree using ggtree (Yu *et al.* 2017). Evolutionary rates through time for all trees were calculated using the variable rates post processor (Baker *et al.* 2016) with 1000 time slices per tree and accounting for shared ancestry as implied by phylogeny (Venditti *et al.*

2011; Sakamoto & Venditti 2018). Mean evolutionary rates through time were calculated for all Lepidosauria and for separate clades (Rhynchocephalia and Squamata). Evolutionary rates were plotted against time using geoscale (Bell 2015).

Evolutionary rates for Rhynchocephalia and Squamata were compared using a phylogenetic analysis of covariance (ANCOVA), accounting for differences in branch lengths. The ANCOVA was run using the root-to-tip pathwise rates as the dependent variable (= sum of mean rate scalars from root to each tip), the two lepidosaur clades as the grouping variable, and time (= sum of path lengths of time-scaled tree from root to each tip) as the covariate. The root-to-tip pathwise rates were \log_{10} -transformed prior to running the phylogenetic ANCOVA. The time-scaled trees stretched by the mean rate scalars served as input phylogenies (see also Avaria-Llautureo *et al.* 2019). Additionally, we used the unmodified time-scaled trees as input phylogenies. For the unmodified time-scaled trees we generated two types of correlation structure assuming no phylogenetic signal (Pagel's $\lambda = 0$; Pagel 1999) and strong phylogenetic signal (Pagel's $\lambda = 1$), respectively. Attempts to estimate Pagel's λ failed for some trees (possibly the result of a flat likelihood surface or because of optimization problems) and were therefore ignored. We implemented the model using the gls() function of the R package nlme v.3.1-140 (Pinheiro *et al.* 2019). Phylogenetic ANCOVAs were run for each time-scaled tree separately. Analyses were repeated for each of the three different topologies.

Body size evolution

Using the fastAnc() function of the R package phytools (Revell 2012) we estimated ancestral body size at internal nodes of the lepidosaur phylogeny. To account for the heterogeneity in evolutionary rates, we calculated a consensus tree for all time-scaled trees (based on the Conrad (2008) topology) in which the branch lengths had been multiplied with the mean rate scalars calculated by BayesTraits. The consensus tree was computed using phytools (Revell 2012). We calculated the resulting mean branch lengths, ignoring edges that were not present in all trees of the chosen topology. This consensus tree then served as input phylogeny for the fastAnc() function to obtain ancestral body size estimates which account for rate heterogeneity. We then generated a phenogram using ggtree (Yu *et al.* 2017) based on the MBL tree, the measured mandible lengths, and the ancestral state estimates. Branches were colour-coded according to the mean rate scalars. Using the loess() function of the R package stats (R Core Team 2013; v.3.6.0) we generated local polynomial regressions using default settings for the measured

\log_{10} -transformed lower jaw lengths through time and plotted the results using geoscale (Bell 2015).

RESULTS

Heterogeneity of rates of evolution

We find that heterogeneous rates of body size evolution characterized early lepidosaurian evolution (Fig. 1), but patterns of body size evolution were consistent for all three alternative supertree topologies tested (see Herrera-Flores *et al.* 2021b). We focus here on the results based on the Hedman time-scaling approach, but similar results were obtained for the FBD time-scaled trees (see Herrera-Flores *et al.* 2021b). The heterogeneous rate model is supported in Bayesian evolutionary rates analyses on 100 time-scaled iterations of each topology of the Conrad

(2008) phylogenetic tree, with positive evidence ($\log(\text{BF}) \geq 2$) in 99 out of 100 trees, strong evidence ($\log(\text{BF}) \geq 5$) in 88 out of 100 trees, and very strong evidence ($\log(\text{BF}) \geq 10$) in 38 out of 100 trees, and for the FBD time-scaled trees, the figures are 99, 96 and 78 out of 100 trees, respectively. For the Gauthier *et al.* (2012) topology, figures are 99, 82, 40 (FBD: 98, 93, and 74), and for the Simões *et al.* (2018) topology, figures are 99, 83, 44 (FBD: 99, 97, and 86). Hence, the proportions are nearly the same for each of the phylogenetic topologies.

For Rhynchocephalia, early diverging taxa have slow rates of body size evolution. However, evolutionary rates for the diverse neosphenodontians are considerably higher, including sphenodontids, the Opisthodontia, a group of specialized herbivores, and pleurosaurs, a group of fully marine taxa (Fig. 1). In squamates, rapid rates of body size evolution are primarily seen in the marine Mosasuroidea (in the FBD trees these high rates are less

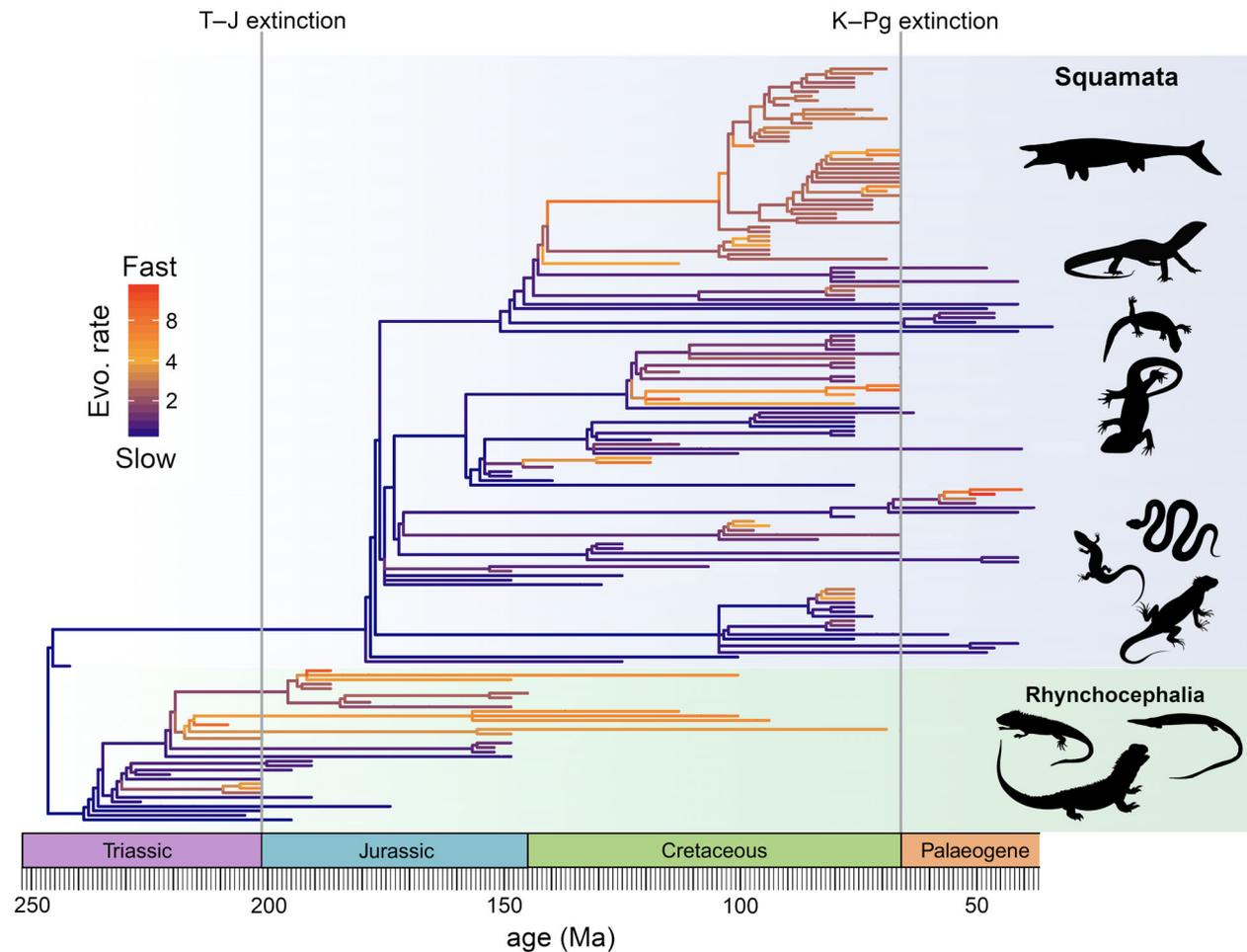


FIG. 1. Rates of lepidosaurian body size evolution through time. Colours from purple to red on the time-calibrated supertree indicate the increase of evolutionary rates in clades (highest rates orange and red), internal and terminal branches. Relationships between higher clades of squamates follow the topology of Conrad (2008). For results using the other squamate topologies see Herrera-Flores *et al.* (2021b); species names at tips are shown in Herrera-Flores *et al.* (2021b) and Figure S31.

prevalent in the tips and more concentrated on the internal branches leading to Mosasuroidea and Mosasauridae; see Herrera-Flores *et al.* 2021b) and the closely related marine Dolichosauridae. High rates are also consistently recovered in polyglyphanodontian scincomorphs, and less consistently in platynotans and Serpentes. All other higher squamate clades are generally characterized by slow evolutionary rates, including the diverse iguanians, gekkotans, and non-polyglyphanodontian scincomorphs (Fig. 1).

Temporal evolutionary rate trends show that rhynchocephalians had notably, and consistently, higher rates of body size evolution than squamates and the pooled rates for all lepidosaurs during the Mesozoic (Fig. 2A). Mean evolutionary rates, from the 100 dated phylogenies, reveal a steady increase in rates of lepidosaurian body size evolution from the Middle Triassic to the Late Jurassic, followed by an abrupt increase in rates during the Late Jurassic and a high plateau in the Early Cretaceous. This trend is mirrored by rhynchocephalians, but the rates were higher for this subclade and the Late Jurassic rate increase and Early Cretaceous plateau are more

exaggerated. In contrast, squamate body size evolutionary rates were stable throughout the Mesozoic and consistently slower, with just two intervals of marked elevated rates in the latest Cretaceous and the Eocene (Fig. 2A; an additional minor peak is seen at the beginning of the Late Cretaceous in the FBD trees; see Herrera-Flores *et al.* 2021b).

Contrasting evolutionary rate dynamics among all lepidosaurs, rhynchocephalians and squamates are confirmed in the distribution of rate parameters for all branches in the 100 dated phylogenies (Fig. 2B). Density plots for the relative evolutionary rates show that rhynchocephalians have a long-tail distribution with a greater relative proportion of both high-rate and low-rate branches compared to squamates. As a whole, Lepidosauria shows an intermediate trend between the two constituent subclades, though the influence of the more speciose squamates dominates. Phylogenetic ANCOVA tests confirm that rhynchocephalians tended to have higher rates than squamates: the groupwise difference in means accounting for the effect of time (= difference in branch length) show

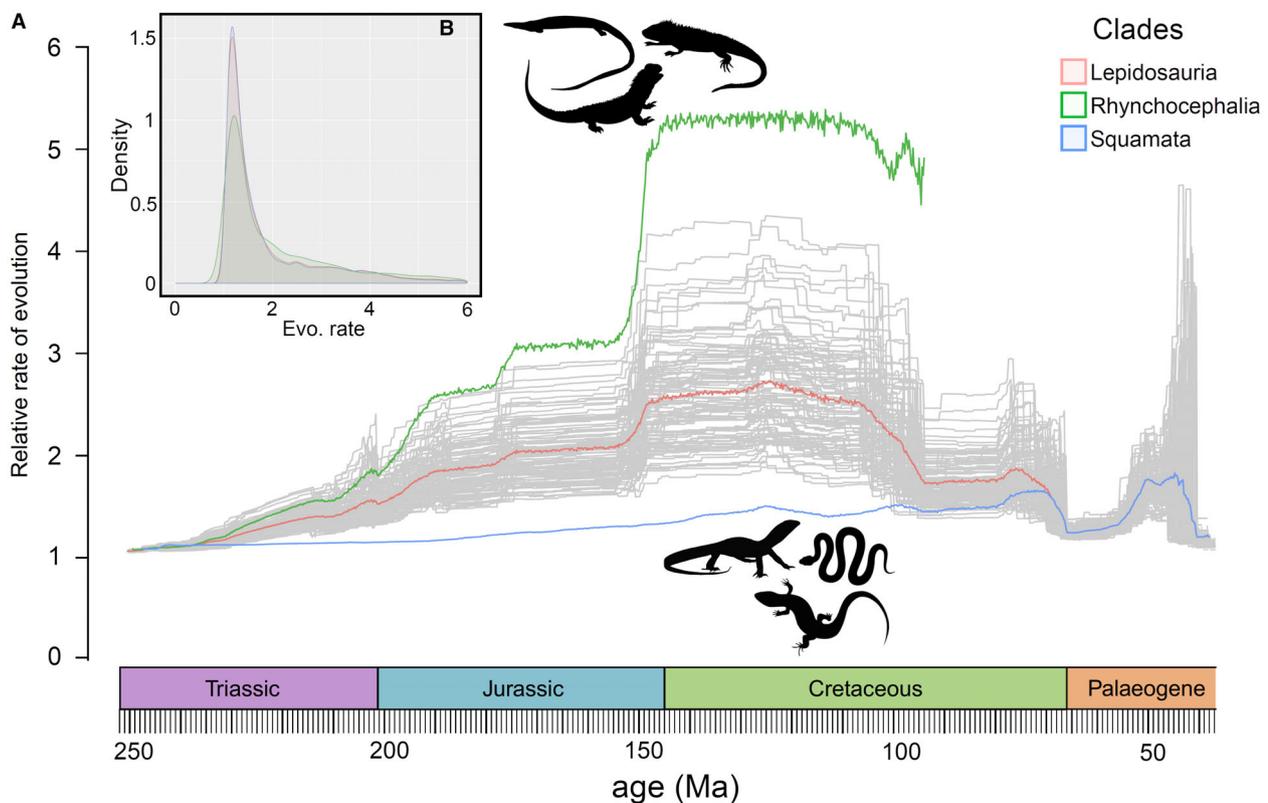


FIG. 2. Mean time-dependent body size evolutionary rates. The values are calculated from 100 trees, using the Conrad (2008) tree, and accounting for shared ancestry; see Herrera-Flores *et al.* (2021b). A, (main plot) mean rates through geological time for all Lepidosauria (red), Squamata (blue) and Rhynchocephalia (green), with scatter of mean rates for Lepidosauria for each of the 100 trees (grey). B, (inset) density plot of relative body size evolutionary rates among lepidosaurs, squamates and rhynchocephalians. Rhynchocephalia show significantly higher rates than Squamata throughout when accounting for differences in branch lengths (see results of phylogenetic ANCOVA).

that the mean evolutionary rate of rhynchocephalians was significantly higher than that of squamates across all 100 Hedman time-scaled trees in all three topologies ($p < 0.05$; see Herrera-Flores *et al.* 2021b). The same applies to nearly all FBD time-scaled trees except for those models in which the correlation structure was based on trees with Pagel's λ forced to 1; in this case, we found no significant difference between the mean evolutionary rates of rhynchocephalians and squamates in 5 out of 100 trees (topology of Conrad 2008), in 6 out of 100 trees (topology of Gauthier *et al.* 2012) and 10 out of 100 trees (topology of Simões *et al.* 2018). The difference of the intercepts corresponds to about two times the background rate of evolution.

Body size evolution through time

The earliest rhynchocephalians were relatively small (~20–30 mm mandible length) and occupied a small-size body size range (Fig. 3A). Already at the end of the Late Triassic, however, they had expanded their morphospace by the addition of tiny carnivorous reptiles like *Clevo-saurus cambrica* (mandible length < 15 mm) and larger herbivores such as *Sphenotitan leyesi* (mandible length > 100 mm). The rapid expansion of their body size range translated into high rates of body size evolution and this pattern continued through the rest of the Mesozoic, with taxa ranging from mandible lengths of ~8 mm (*Zapaton ejidoensis*) to 115 mm (*Kawasphenodon expectatus*). Rhynchocephalians achieved body sizes close to both the minimum and maximum of non-mosasauroid Mesozoic squamates, exceeding their squamate counterparts during several stratigraphic stages (Fig. 3A, B). The rapid expansion of occupied ecological niches, ranging across several categories of insectivory and herbivory, evidenced by the high evolutionary rates, however, did not translate into success in the long term.

On the other hand, non-mosasauroid Squamata evolved to fill different body size niches in a much more gradual fashion, with overall lower rates of body size evolution (Fig. 3A, B). While ultimately attaining a body size range similar to Rhynchocephalia, with a minimum mandible length of ~6 mm (*Olindalacerta brasiliensis*) and maximum of ~145 mm (*Estesia mongoliensis*), non-mosasauroid squamates were smaller than their rhynchocephalian counterparts during most of the Mesozoic. The body size of the marine Mosasauroida was extreme relative to other lepidosaurs, ranging from 130 mm (*Aigialosaurus dalmaticus*) to 1710 mm (*Mosasaurus hoffmannii*) lower jaw length. The body size of mosasauroids evolved faster compared to other squamates allowing them to quickly enter different ecological niches (ambush and pursuit fish-eating predators, mollusc-eaters) in their

distinct body size morphospace. Similar to rhynchocephalians, however, the ability to invade different body size niches rapidly did not guarantee long-term success and the clade went extinct at the end of the Cretaceous.

To summarize body-size trends (Fig. 3B), lepidosaurs began small in the Triassic, with rhynchocephalians expanding to large sizes first, at the end of the Triassic. Mean body size for squamates (Fig. 3B, blue line; orange line, excluding mosasauroids) declined slightly through the Jurassic and Cretaceous, but that decline reflects body sizes of rare squamates, whereas rhynchocephalian mean body size increased throughout the Mesozoic. The peak in squamate body size in the Late Cretaceous is driven by mosasauroids and polyglyphanodontians, and the Palaeogene drop by their extinction.

DISCUSSION

We confirm here that during the first two-thirds of their history, rhynchocephalian body size evolved much faster than squamate body size. Yet rhynchocephalian diversity declined through the Cretaceous, and the switch to low diversity and potentially lower evolutionary rates in rhynchocephalians may have been mediated by the K–Pg event, or is very likely to have occurred some 40 myr earlier, at the beginning of the Late Cretaceous; we cannot say because their fossil record is too sparse to be sure. What is new here is that we have shown that their initial success was sustained through unusually high rates of evolution through most of their history in the Mesozoic, and that squamates retained slow evolutionary rates through that time.

Why such marked differences in evolutionary rates, and why did rhynchocephalians apparently give way to squamates? Some authors have suggested competition, with the rise of squamates, especially lizards, creating competition for resources between the two groups (Saint Girons *et al.* 1980; Milner *et al.* 2000; Apesteguía & Rougier 2007). Others (Gorniak *et al.* 1982; Whiteside 1986; Jones 2006) have suggested competition with mammals, or changing environments whereby early rhynchocephalians were adapted to more arid environments, and early squamates to more mesic environments (Evans 1995, 2003). At the very least, if there had been competition the two clades might be expected to have waxed and waned over the same time interval, but that is not evident: rhynchocephalians declined in diversity in the Late Jurassic and Early Cretaceous, well before the expansion of squamate diversity (Herrera-Flores *et al.* 2021a). Second, their diets and other habits might be expected to have overlapped in some way so that a plausible case for competition for resources could be made; this is also not the case (Jones 2008; Evans & Jones 2010; Herrera-Flores

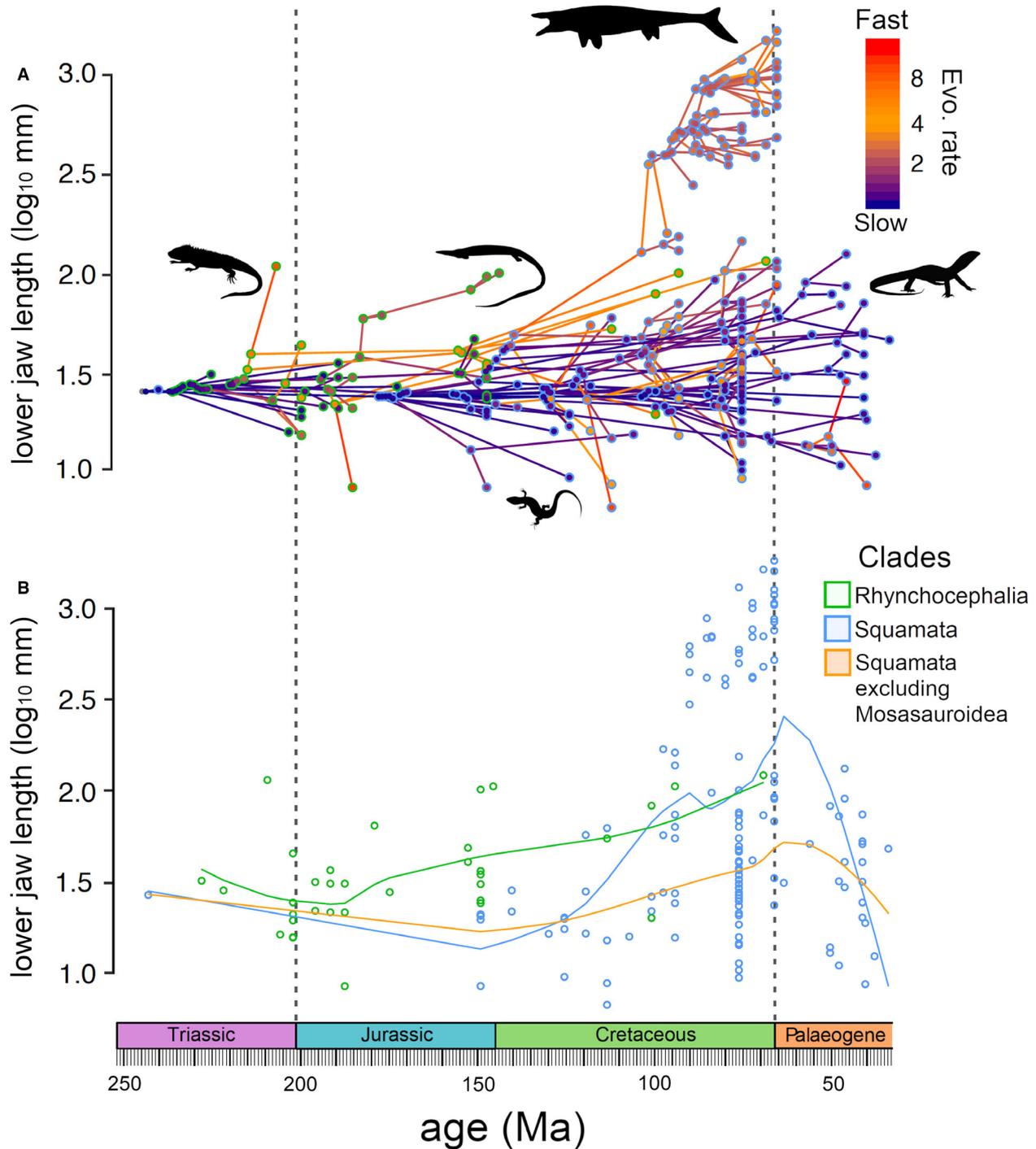


FIG. 3. Body size evolution of early lepidosaurs. A, phenogram of early lepidosaur body size is based on the Conrad (2008) topology for major squamate clades; tips and internal nodes are colour-coded according to clade assignment (green = Rhynchocephalia; blue = Squamata), and branches are colour-coded according to relative rates of body size evolution. B, lepidosaur body size through time; local polynomial regressions for Rhynchocephalia (green), Squamata (blue), and Squamata excluding Mosasauroida (orange).

et al. 2017). Perhaps the two groups changed their relative macroecological roles for a variety of reasons, including intraspecific competition at times as well as environmental changes (Evans 1995, 2003).

Many studies suggest an association of high rates of phenotypic evolution with high biodiversity, since quickly evolving clades might be expected to be faster to invade the available niche space. Indeed, studies of morphological

evolution in dinosaurs (Benson *et al.* 2014), actinopterygian fishes (Rabosky *et al.* 2013), crocodylomorphs (Stubbs *et al.* 2021) and crustaceans (Adamowicz *et al.* 2008), and genome size evolution in plants (Puttick *et al.* 2015), have linked the evolutionary success of clades to rapid evolutionary rates and ‘evolvability’. In contrast, slow evolutionary rates, in this case mediated by low origination rates, apparently contributed to the extinction of ichthyosaurs; a once diverse clade of marine reptiles (Fischer *et al.* 2016; Moon & Stubbs 2020). Therefore, it is predicted that phenotypic evolvability, or greater evolutionary versatility, should promote speciation and make clades more persistent on macroevolutionary timescales (Vermeij 1973; Rabosky *et al.* 2013).

Simpson’s (1944) seemingly contrarian view was that slow rates would mean low levels of volatility and so less risk of extinction: ‘slow and steady wins the race’. He established the notions of tachytely (fast rates), bradytely (slow rates) and horotely (average rates), and argued (Simpson 1944, p. 134) that tachytelic lineages ‘cannot endure as such, but must soon either become extinct or become horotelic or bradytelic.’ He argued that tachytelic clades would be highly volatile, fast changing and so rare as fossils.

Heterogeneity of evolutionary rates is well established, but only a few cases (Myers 1960; MacFadden 1988; Schopf 1994; Simões *et al.* 2020a) show slow rates in a diverse clade, and we know of no example that supports Simpson’s (1944) prediction about the extinction of groups with high rates of phenotypic evolution sustained over long periods of time. We found that among the three models of distribution of evolutionary rates proposed by Simpson (1944), the tachytelic model seems to fit the fast evolution and subsequent decline of some larger clades of lepidosaurs. Previous studies have suggested tachytelic evolution in some lineages of extant fishes and bacteria (Myers 1960; Woese *et al.* 1985; Morse *et al.* 1996), but none of these shows the entire process of Simpson’s tachytelic evolution, in that they must become horotelic, bradytelic or extinct (Simpson 1944). Rhynchocephalia was highly successful, but nearly became extinct after the Early Cretaceous (Apesteguía *et al.* 2014; Herrera-Flores *et al.* 2017; Cleary *et al.* 2018). As noted, we cannot find evidence that their decline was caused by the rise of lizards, nor that their near extinction was caused by sustained high rates of evolution. Only two rhynchocephalian lineages survived beyond the K–Pg boundary: the opisthodontian *Kawaphenodon* that survived until the early Paleocene (Apesteguía *et al.* 2014) and the extant tuatara *Sphenodon* from New Zealand. Previous evolutionary rate analysis (e.g. Herrera-Flores *et al.* 2017; Simões *et al.* 2020b) suggested that Sphenodontinae, the lineage that includes *Sphenodon* and its close relatives, experienced long-term morphological stasis after the Jurassic, which also coincides

with Simpson’s (1944) statement that tachytelic taxa can later become horotelic or bradytelic.

In addition to high rates in Rhynchocephalia, our analyses also identified elevated rates in the Mosasauroidae + Dolichosauridae squamate clade and polyglyphanodontian squamates. These clades, particularly the mosasaurs, were highly successful in the Late Cretaceous but also became extinct. The Simpsonian model of change in evolutionary rates may also apply to these squamate clades. However, in contrast to rhynchocephalians, whose decline began long before the K–Pg boundary (Apesteguía *et al.* 2014; Herrera-Flores *et al.* 2017; Cleary *et al.* 2018), the extinction of mosasaurs and polyglyphanodontians has been attributed to the K–Pg mass extinction event (Longrich *et al.* 2012; Polcyn *et al.* 2014).

Our work offers a novel exploration of the decline of rhynchocephalians in the Cretaceous and suggests that the longevity and ecological dominance of squamates cannot be attributed to rapid rates of body size evolution at their origin. Our finding is analogous to that of Clarke *et al.* (2016) who showed that teleosts, today by far the most species-rich group of bony fishes (*c.* 29 000 species), initially showed lower rates of evolution than the holosteans, today represented by only eight species. Indeed, the living holosteans, like the rhynchocephalians, have often been dubbed ‘living fossils’, reflecting their low current species richness and apparent slow taxic evolutionary rates through the Cenozoic. Simpson’s classic proposal for links between evolutionary rates, and long-term persistence and success previously lacked empirical examples using modern computational macroevolutionary techniques, and most other quantitative studies have suggested that rapid evolutionary rates are key to long-term success; we find the opposite was true for Lepidosauria.

CONCLUSIONS

1. We explored body size evolution in a sample of 167 Mesozoic lepidosaurs, including all taxa for which mandible data exists, with the aim of comparing the two major clades, Rhynchocephalia and Squamata.
2. Phylogenetic comparative analyses show substantial heterogeneity in evolutionary rates throughout both subclades.
3. Further, there is a clear distinction between the two clades, with rates of evolution substantially higher in Rhynchocephalia than in Squamata and sustained throughout the Mesozoic.
4. These mean Mesozoic rates differ substantially from rates in the Cenozoic and today, where rhynchocephalians comprise a single species that underwent generally slow evolution in the past 66 million years,

compared to squamates with over 10 000 species today and generally fast rates of evolution.

5. The findings confirm a prediction by Simpson (1944) that fast evolving (tachytelic) clades would not necessarily lead to high diversity because of their volatility and the likelihood that fast rates could not be sustained and would switch to average or slow rates.

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DATA ARCHIVING STATEMENT

Data for this study are available in the Dryad Digital Repository: <https://doi.org/10.5061/dryad.j0zpc86f5>

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SUPPORTING INFORMATION

Additional Supporting Information can be found online (<https://doi.org/10.1111/pala.12579>):

Appendix S1. Includes Nexus file and additional evolutionary rate figures (Figs S1–S31).

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