ORIGINAL ARTICLE

Asian Herpetological Research 2021, 12(3): 289–294
DOI: 10.16373/j.cnki.ahr.210018

Effects of Life Histories on Genome Size Variation in Squamata

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Abstract Genome size changes significantly among taxonomic levels, and this variation is often related to the patterns shaped by the phylogeny, life histories and ecological factors. However, there are mixed evidences on the main factors affecting molecular evolution in animals. In this study, we used phylogenetic comparative analysis to investigate the evolutionary rate of genome size and the relationships between genome size and life histories (i.e., hatchling mass, clutch size, clutches per year, age at sexual maturity, lifespan and body mass) among 199 squamata species. Our results showed that the evolutionary rate of genome size in Lacertilia was significantly faster than Serpentes. Moreover, we also found that larger species showed larger hatchling mass, more clutches per year and clutch size and longer lifespan. However, genome size was negatively associated with clutch size and clutches per year, but not associated with body mass we looked at. The findings suggest that larger species do not possess the evolution of large genomes in squamata.

Keywords genome size, body mass, evolutionary rate, life histories

1. Introduction

Genome sizes vary considerably across taxa in organisms (Cavalier-Smith, 1978; Bennett and Leitch, 2005; Lynch and Walsh, 2007). This can be driven by the stochastic genetic and/or genomic processes associated with spontaneous deletions and/or insertions, polyploidization, prolonged tandem repeats length, transposable elements number and genetic drift, but can be also shaped by natural selection (Ogata *et al*., 1996; Petrov, 2001; Sun *et al*., 2012; Lynch, 2011; Whitney and Garland, 2010). In particular, genome size variations are mainly explained by two important mechanisms including the duplication events and the proliferations of noncoding elements (Neiman *et al*., 2015). Establishing the association between genome size variation and organismal complexity has puzzled many evolutionary biologists and as such remains a classic problem in biology (Gregory, 2005a).

Previous studies across taxa have revealed positive associations between genome size and cell size, nucleus size, developmental time, nutrient requirements, tissue differentiation, life cycle complexity and body size (Vinogradov, 1997; Olmo and Morescalchi, 1978; Gregory, 2005a; Gregory, 2001; Gregory and Johnston, 2008; Guignard *et al*., 2016). These positive associations have been suggested to be consequences of both the cytoplasm from more efficient mRNA transport and larger cells necessitating larger genomes based on structural causes (Cavalier-Smith, 1985). Smaller cells for instance, usually divide faster and have a higher metabolic rate, evidenced by a negative correlation between metabolic rates and DNA amounts in mammals and birds (Hughes and Hughes, 1995; Vinogradov, 1995; Gregory, 2002a; Hughes and Piontkivska, 2005). However, a potential correlation which still needs to be explored between cell volume and genome size is body size

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Received: 20 March 2021 Accepted: 21 August 2021

(Gregory *et al*., 2000).

Body size variation is often determined either by cell size and cell number, or both combination in organisms (Hessen *et al*., 2013; Kozłowski *et al*., 2003). For plants and animals, genome size displays a positive association with cell size (Gregory *et al*., 2000; Bennett, 1987; Gregory, 2005b). In addition, this correlation can be often linked to ecological factors. For example, genome size exhibits a positive association with body size in some invertebrates (e.g., amphipods, copepods, crustaceans) due to low metabolic rate and temperatures in cold waters (Rees *et al*., 2008; Angilletta *et al*., 2004; Timofeev, 2001; Jeffery *et al*., 2016; Leinaas *et al*., 2016). Genome size variation in frogs is indirectly affected by temperature and humidity as a result of its influence on the time of premetamorphic development (Liedtke *et al*., 2018). In birds, mitochondrial and nuclear of substitution rate in coding sequences reveal weak negative associations between the ratio of nonsynonymous and synonymous substitution rate and age at sexual maturity, lifespan and body mass associated with environmental factors (Weber *et al*., 2014; Lanfear *et al*., 2010; Nabholz *et al*., 2013), but it is not always the case (Figuet *et al*., 2017).

Squamata constitutes the class of vertebrates with a small genome size due to a lower fraction of transposable elements and shorter introns (Organ *et al*., 2007). However, this may be a misconception caused by overlooking GC-rich regions, which are often hard to access (Botero-Castro, 2017). Ploidy variations does not provide a major power of variation in genome size, and the whole-genome duplication events is not reported during the amniote evolutionary process in squamata (Van de Peer *et al*., 2009). Squamata mainly consists of two suborders (e.g., Lacertilia and Serpentes) and displays complex life histories with prolonged developmental periods (hatching time), which likely constrains the variation of genome size because of a negative correlation between genome size and development time in invertebrates (Wyngaard *et al*., 2005).

To examine the selective mechanisms underlying genome size variation in squamata, we first estimated the evolutionary rates of genome size between Lacertilia and Serpentes in squamata. We also expanded our extent to which genome size can be considered as a determinant of life histories by investigating the relationships between variation in genome size and life histories among 199 squamata species. We tested whether larger bodies can promote evolution of larger genomes.

2. Materials and Methods

2.1. Data collection The genome size of 199 squamata species was collected from genome size database (http://www.genomesize.com) (supplementary Information: Table S1). We extracted data on genome size for squamata species for which information on life histories can be found (see below), and obtain their average *C*-value. We used average values of genome size when more than one measurement per species was available. To avoid possible errors due to several methods being used to quantify genome size (Hardie *et al*., 2002), we used parallel analyses on a subset of genome size. We confirmed species names using the NCBI taxonomy database, and collapsed/pruned all synonyms from the phylogenetic tree. We rebuilt the phylogenetic tree using time-calibrated molecular phylogeny by Pyron *et al*. (2013) (Figure 1) and examined difference in the evolutionary rate of genome size between Lacertilia and Serpentes. Finally, we compiled information on hatching time, hatchling mass, clutch size per year, clutch size and body mass (see details in De Smet, 1981; Feldman *et al*., 2016; Allen *et al*., 2017) and age at sexual maturity, lifespan from the AnAge databases (https://genomics.senescence.info/species/) (supplementary Information: Table S1).

2.2. Statistical analyses The complementary approaches were used to evaluate the evolution rate of genome size for three suborders. For each suborder, we assessed phylogenetic signal using the *phylosig* function in the package of *phytools* in RStudio v.3.1.2 (Revell, 2012). We then used the Blomberg's *K* (Blomberg *et al*., 2003) in which genome size variation comparing on a null model is assumed genome size evolution under Brownian motion (BM) model. We also used the Pagel's λ (Pagel, 1999) in which phylogenetic signal is estimated on the basis of the phylogenetic dependence of genome size. $K = 1$ indicated genome size evolved as expected under a BM model, while $K > 1$ or $K < 1$ indicated less or more phylogenetic signal than expected under a BM model, respectively. We used Blomberg's *K* and Pagel's λ to estimate the phylogenetic signal and found qualitatively similar results (Table S2).

We used the *fitContinuous* function in the R package-*Geiger* (Harmon *et al*., 2008) to compare genome size evolution on the basis of Brownian motion, Ornstein-Uhlenbeck and Early-burst models between the two suborders. Following the suggestions by Simmons and Fitzpatrick (2016), BM model of genome size evolution was regarded to be the best model due to small sample size. Moreover, to compare differences in evolutionary rate of genome size between the two suborders, we modified a likelihood method where a phylogeny can directly compare on the Brownian evolutionary rate (σ^2) of genome size (Adams, 2013).

To examine associations between genome size and life histories, we used the phylogenetic generalized least squares models where the phylogenetic structure of the model residuals was considered in the *caper* package (Orme *et al*., 2012; Huang *et al*., 2020). We used phylogenetic scaling parameter λ to estimate the phylogenetic influence on the associations between genome size and life histories based on a maximum-likelihood approach (Pagel, 1999). The scale of λ-values ranges from zero (i.e., phylogenetic independence) to one (i.e., complete phylogenetic non-independence) (Freckleton *et al*., 2002; Mai *et al*., 2019). We $\log_{10}$-transformed life histories to linearize associations and used the phylogenetic tree of squamata species to correct for phylogenetic dependence (Mai *et al*., 2020). To test the associations between body mass and life histories, we treated body mass as response variable, hatchling mass, clutches per year, clutch size, age at sexual maturity and lifespan as predictor variables using the multivariate phylogenetic generalized least squares. To test whether genome size exhibited a association with body mass, we treated body mass as predictor variable, genome size as response variable, and hatchling mass, clutches per year, clutch size and lifespan as covariates using the multivariate phylogenetic generalized least squares.

3. Results

The average value of genome size was 2.11 pg, ranging from 1.19 to 3.93 pg among 199 species of squamata. Genome size in Lacertilia tended to be larger than that in Serpentes (Figure 2). The evolutionary rate of genome size in Lacertilia was faster than that in Serpentes (Table S3).

The multivariate phylogenetic generalized least squares model indicated that body mass was positively associated with hatchling mass, clutches per year, clutch size and lifespan among 199 species of squamata (Table 1) . The genome size was not associated with body mass when the effects of hatchling mass, clutches per year, clutch size and lifespan were removed (Table 2). We also found negative correlations between genome size and clutch size or clutches per year (Table 2).

For Serpentes in particular, body mass was positively and

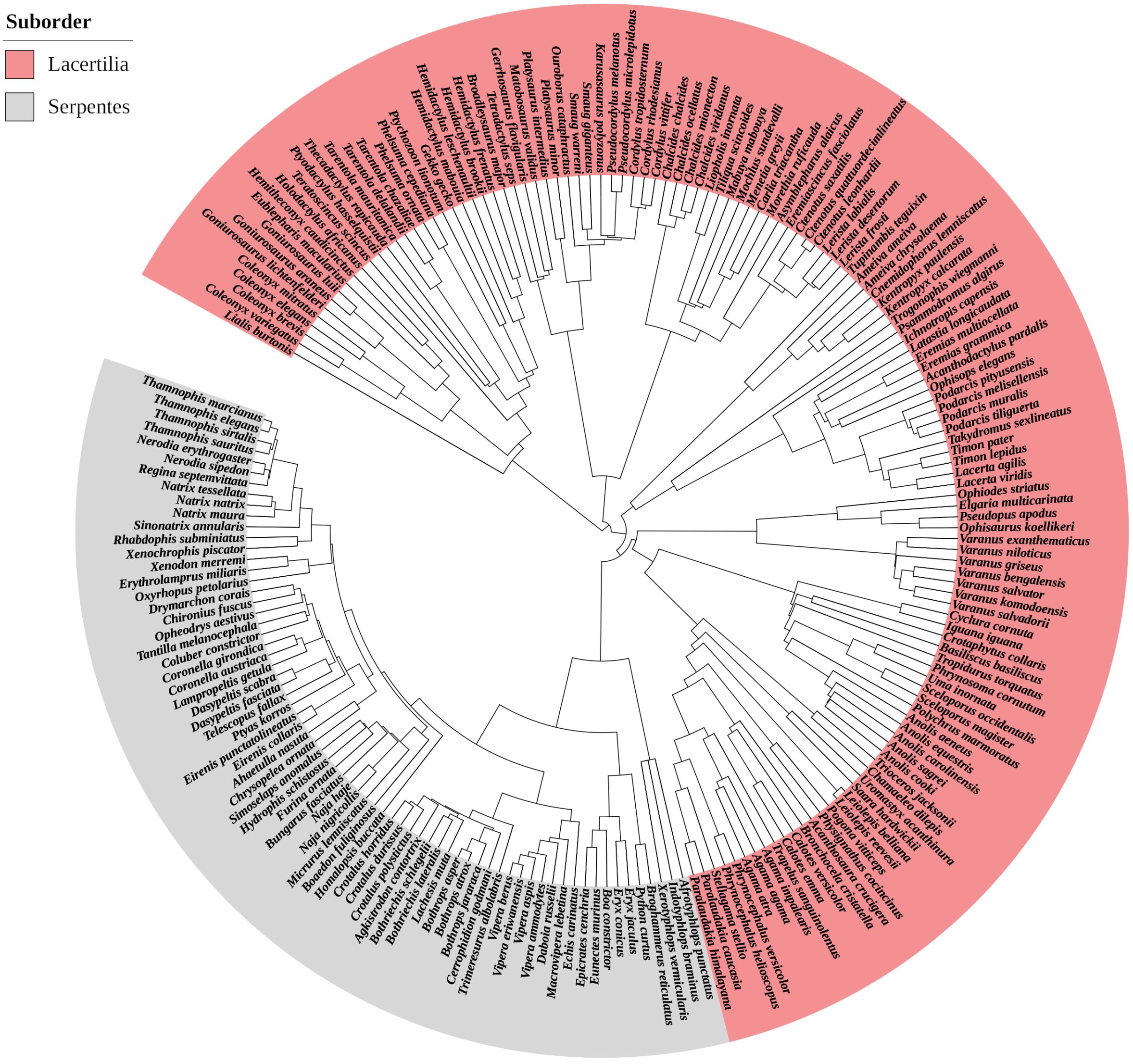

Figure 1 The phylogenetic tree of the 199 species of squamata used in the comparative analysis.

significantly associated with hatchling mass and clutch size, but not with clutches per year, age at sexual maturity and lifespan using the multivariate phylogenetic generalized least squares model (Table S4). However, there was no association between genome size and body mass when removing the hatchling mass and clutch size effects (Table S5). For Lacertilia, body mass was significantly associated with hatchling mass, clutches per year, clutch size and lifespan (Table S4). When the influences of hatchling mass, clutches per year, clutch size and lifespan were removed, we found no association between genome size variation and body mass (Table S5).

Table 1 The associations between body mass and life histories across 199 species of squamata. Phylogenetic scaling parameters (superscripts following λ denote *P*-values of likelihood ratio tests against models with $\lambda = 0$ and $\lambda = 1$, respectively).

Predictors	Body mass				
	λ	β	t	R^2	P
Hatchling mass	$<0.001^{1,0.0016}$	1.001	9.543	0.791	<0.001
Clutch size		0.811	5.059	0.516	<0.001
Clutches per year		0.530	2.293	0.180	0.031
Age at sexual maturity		−0.372	−1.541	0.090	0.136
Lifespan		0.481	2.947	0.266	0.007

Table 2 The associations between genome size and life histories across 199 species of squamata. Phylogenetic scaling parameters (superscripts following λ denote P-values of likelihood ratio tests against models with $\lambda = 0$ and $\lambda = 1$, respectively).

Predictors	Genome size				
	λ	β	t	R^2	P
Body mass	$<0.001^{1,<0.001}$	0.090	1.865	0.110	0.073
Hatchling mass		−0.087	−1.392	0.065	0.175
Clutch size		−0.231	−3.920	0.354	<0.001
Clutches per year		−0.146	−2.124	0.139	0.043
Lifespan		0.028	0.565	0.011	0.576

4. Discussion

Our results showed that genome size evolution in Lacertilia evolved significantly faster than that in Serpentes among 199 species of squamata. We found positive correlations between body mass and hatchling mass, clutches per year, clutch size, and lifespan. However, genome size was not associated with body mass when correcting for the effects of part life histories. For Lacertilia and Serpentes, genome size did not show a association with body mass.

Differences in transposable element accumulation rates in animals experienced may lead to substantial variation in genome size among species (Chalopin *et al*., 2015; Gibbs *et al*., 2004). For example, a number of DNA obtained by transposable element accumulation with strong changes among lineages, are counteracted by loss of DNA on the basis of large segmental deletion in birds (Kapusta *et al*., 2017). For 199 species of squamata, the rate of transposable element accumulation can also explain the marked variation in genome size, ranging from 1.19 to 3.93 pg.

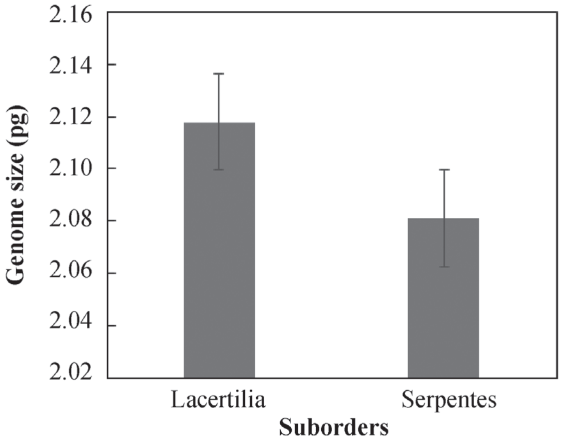

Figure 2 Genome size difference between Lacertilian and Serpentes for 199 species of squamata.

The evolutionary history of genome size in amphibians has been one of gradual, time-dependent variation (Brownian motion; Liedtke *et al*., 2018). In this study, evolutionary model-fitting showed that genomes in Lacertilia and Serpentes evolved under a shared processes of Brownian motion. The common ancestor of extant squamata was predicted to have similar size in genome in Lacertilia and Serpentes. We inferred that genome size in squamata evolved gradually as a function of time (Brownian motion). Herein we found that the evolutionary rate of genome size in Lacertilia evolved faster than Serpentes. Palaeontological data and genomic evidence display a similar pattern (Pyron *et al*., 2013).

There are evidences that phylogeny is likely to promote the influences of genome duplications and transposons on genome size evolution in animals (mammals: Tang *et al*., 2019; insects: Alfsnes *et al*., 2017). For example, genome size is phylogeny-dependent when $\lambda > 0.9$ in all life-history traits is reported in mammals (Tang *et al*., 2019). However, phylogeny displays a weak correlation with genome size in crustaceans (Alfsnes *et al*., 2017). Likewise, there is a weak association between genome size and phylogeny among 240 species of birds when $\lambda \leq 0.564$ is recorded in all life-history traits (Yu *et al*., 2020). We found that genome size was not associated with phylogeny, suggesting that the phylogeny did not a strong power in driving transposons and duplications of genome in squamata.

Genome size variation can be explained by the more mechanistic and/or short period effects which is regarded as the proximate causes. Moreover, the evolutionary powers (i.e., selection), regarding as the ultimate causes, can also explain the genome size variation (Hessen *et al*., 2013; Alfsnes *et al*., 2017; Yu *et al*., 2020). For birds, variations in genome size are positively related to the length of developmental period (Kapusta *et al*., 2017; Yu *et al*., 2020), providing evidence for the associations between life histories and genome size evolution. Indeed, genome size displays markedly and directly effects on cell size and cell replication rate (Gregory, 2002b), so larger genomes are expected to be positively correlated with larger egg size and smaller clutch size. However, large datasets have indicated that variations in genome size are not associated with offspring number and size in mammals (Tang *et al*., 2019) and life history complexity of amphibians (Liedtke *et al*., 2018). In this study, there were negative correlations between genome size variation and life histories such as clutch size and clutches per year in squamata, suggesting that less offspring number or larger offspring size can promote evolution of larger genomes.

Body mass is positively associated with genome size in vertebrates (Liedtke *et al*., 2018; Tang *et al*., 2019; Yu *et al*., 2020) and invertebrates (Gregory *et al*., 2000; McLaren *et al*., 1989; Hessen and Persson, 2009; Alfsnes *et al*., 2017). Such positive associations between cell size and genome size (Gregory, 2005a; McLaren and Marcogliese, 1983) have indicated that variations in body size among the related species can partly respond to variation in cell size (Hessen *et al*., 2013). Indeed, genome size exhibits positively correlations with body mass in birds and mammals (Tang *et al*., 2019; Yu *et al*., 2020). Across 199 species of squamata, there were not associations between genome size and body mass, suggesting that diversity in genome size was not response of variation in cell size.

In conclusion, we illustrated the relationships between genome size and life histories in squamata. The hatching time, hatchling mass, clutch size per year and clutch size cannot shaped the genome size variation, and species with larger bodies did not possess larger genomes in squamata. Our future research would need more species to reveal the relationships between genome size evolution and life histories.

Acknowledgements We thank C. L. MAI and J. P. YU to help the data collected. Financial support was provided by the National Natural Sciences Foundation of China (31772451; 31970393) and the Science and Technology Youth Innovation Team of Sichuan Province (2019JDTD0012).

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Handling Editor: Chen YANG

How to cite this article:

Chen C., Jin L., Jiang Y., Liao W. B. Effects of Life Histories on Genome Size Variation in Squamata. Asian Herpetol Res, 2021, 12(3): 289–294. DOI: 10.16373/j.cnki.ahr.210018

Appendix

Table S1 TSpecies, body mass (g), genome size (pg), hatchling mass (g), clutch size, clutches per year among 199 species of squamata from the references of De Smet (1981), Feldman *et al*. (2016), Allen *et al*. (2017), and age at sexual maturity (years) and lifespan (years) from AnAge (https://genomics.senescence.info/species/).

Species	Suborder	Genome size	Body mass	Hatchling mass	Clutch size	Clutches per year	Age at sexual maturity	Lifespan
Acanthodactylus pardalis	Lacertilia	1.44	5.32	0.63	3.68	2.57	1.80	4.00
Acanthosaura crucigera	Lacertilia	1.45	130.31	NA	14.00	NA	NA	2.60
Afrotyphlops punctatus	Serpentes	1.89	251.52	NA	NA	NA	NA	0.30
Agama agama	Lacertilia	1.70	16.61	0.64	8.12	2.00	1.27	8.00
Agama atra	Lacertilia	1.47	15.69	0.38	12.50	NA	NA	NA
Agama impalearis	Lacertilia	1.51	26.77	0.46	11.80	2.13	1.00	6.00
Agkistrodon contortrix	Serpentes	1.37	217.20	10.60	6.50	0.80	2.50	29.80
Ahaetulla nasuta	Serpentes	2.07	681.26	NA	NA	NA	NA	NA
Ameiva ameiva	Lacertilia	2.04	53.21	1.59	5.22	2.25	0.50	4.60
Ameiva chrysolaema	Lacertilia	2.45	17.21	NA	NA	NA	NA	NA
Anolis aeneus	Lacertilia	1.76	2.14	0.25	1.00	NA	NA	NA
Anolis carolinensis	Lacertilia	2.29	2.30	0.22	1.48	9.00	0.62	7.20
Anolis cooki	Serpentes	1.79	210.00	NA	NA	NA	NA	3.30
Anolis equestris	Lacertilia	1.89	56.00	1.95	1.00	6.50	0.80	16.50
Anolis sagrei	Lacertilia	1.89	5.10	0.09	1.50	19.00	0.77	8.00
Asymblepharus alaicus	Lacertilia	1.93	5.36	NA	NA	NA	NA	NA
Basiliscus basiliscus	Lacertilia	2.06	250.00	1.44	10.10	5.56	1.49	7.00
Boa constrictor	Serpentes	2.31	4589.35	145.00	32.67	0.75	3.50	40.40
Boaedon fuliginosus	Serpentes	1.51	315.09	NA	NA	NA	NA	NA
Bothriechis lateralis	Serpentes	1.91	521.19	NA	NA	NA	NA	12.50
Bothriechis schlegelii	Serpentes	1.91	102.00	3.55	13.20	1.50	2.00	19.50
Bothrops asper	Serpentes	2.71	7499.04	NA	29.90	NA	NA	20.40
Bothrops atrox	Serpentes	1.82	1803.45	18.92	31.00	NA	NA	20.20
Bothrops jararaca	Serpentes	2.25	2046.39	NA	12.00	NA	NA	6.50
Broadleysaurus major	Lacertilia	3.36	386.88	NA	5.00	NA	NA	24.00
Broghammerus reticulatus	Serpentes	1.60	21884.68	112.57	76.50	0.63	3.00	29.40
Bronchocela cristatella	Lacertilia	2.38	18.32	1.00	2.00	NA	NA	NA
Bungarus fasciatus	Serpentes	2.38	1777.07	16.87	9.00	NA	NA	13.20
Calotes emma	Lacertilia	2.10	22.17	0.71	7.50	NA	NA	0.70
Calotes versicolor	Lacertilia	1.83	23.80	0.24	14.61	2.25	0.86	5.00
Carlia triacantha	Lacertilia	1.41	1.35	0.14	2.00	NA	NA	NA
Cerrophidion godmani	Serpentes	2.20	294.63	NA	7.00	0.50	NA	15.80
Chalcides chalcides	Lacertilia	1.68	11.92	0.72	7.20	1.00	2.40	4.00
Chalcides mionecton	Lacertilia	1.57	4.30	NA	NA	NA	NA	NA
Chalcides ocellatus	Lacertilia	2.46	21.60	1.15	7.00	1.45	2.40	14.00
Chalcides viridanus	Lacertilia	1.75	24.08	0.65	4.00	1.00	NA	NA
Chamaeleo dilepis	Lacertilia	2.21	40.04	1.04	38.90	1.00	1.00	4.00
Chironius fuscus	Serpentes	2.24	70.00	NA	NA	NA	NA	NA
Chrysopelea ornata	Serpentes	2.00	145.00	1.67	9.00	NA	NA	4.30
Cnemidophorus lemniscatus	Lacertilia	1.42	3.89	0.45	2.11	2.17	0.50	
Coleonyx brevis	Lacertilia	2.01	3.20	0.19	2.00	2.47	1.00	5.00
Coleonyx elegans	Lacertilia	1.56	11.20	0.95	2.00	2.73	NA	11.00
Coleonyx mitratus	Lacertilia	1.76	12.10	0.73	2.00	NA	NA	NA
Coleonyx variegatus	Lacertilia	1.92	3.90	0.30	2.00	2.13	0.90	34.80
Coluber constrictor	Serpentes	1.43	182.00	5.60	13.60	1.00	2.50	10.00
Cordylus rhodesianus	Lacertilia	3.62	9.33	0.84	NA	NA	NA	NA
Cordylus tropidosternum	Lacertilia	3.51	8.03	0.62	2.50	NA	NA	7.90
Cordylus vittifer	Lacertilia	2.87	15.38	2.58	2.50	NA	NA	7.50
Coronella austriaca	Serpentes	1.89	50.00	1.60	9.00	0.40	4.00	12.00
Coronella girondica	Serpentes	2.58	55.00	0.87	11.00	1.00	3.50	16.00
Crotalus durissus	Serpentes	1.32	1795.25	13.73	10.25	NA	3.00	19.80

(Continued Table S1)

Species	Suborder	Genome size	Body mass	Hatchling mass	Clutch size	Clutches per year	Age at sexual maturity	Lifespan
Crotalus horridus	Serpentes	1.75	581.90	22.50	9.70	0.50	6.25	30.20
Crotalus polystictus	Serpentes	1.83	86.80	8.70	7.30	1.00	3.00	5.20
Crotaphytus collaris	Lacertilia	2.38	37.10	1.08	6.38	1.90	0.80	10.00
Ctenotus leonhardii	Lacertilia	1.65	9.14	0.40	4.50	NA	NA	7.00
Ctenotus quattuordecimlineatus	Lacertilia	1.59	5.76	0.40	3.58	NA	NA	NA
Ctenotus saxatilis	Lacertilia	1.50	22.23	NA	NA	NA	NA	NA
Cyclura cornuta	Lacertilia	1.80	4134.50	47.35	13.63	1.00	6.50	22.90
Daboia russelii	Serpentes	2.07	675.00	9.94	34.50	NA	NA	15.00
Dasypeltis fasciata	Serpentes	1.61	167.15	NA	NA	NA	NA	NA
Dasypeltis scabra	Serpentes	1.47	15.70	2.81	15.50	1.50	NA	22.10
Drymarchon corais	Serpentes	2.17	1759.00	22.39	9.00	NA	NA	25.50
Echis carinatus	Serpentes	1.30	170.00	3.68	10.20	NA	NA	9.00
Eirenis collaris	Serpentes	1.80	5.52	0.50	NA	NA	NA	NA
Eirenis punctatolineatus	Serpentes	1.86	10.83	0.48	NA	NA	NA	NA
Elgaria multicarinata	Lacertilia	1.98	31.60	1.05	11.20	1.73	1.50	15.00
Epicrates cenchria	Serpentes	2.66	829.60	42.85	21.50	1.00	NA	31.00
Eremias grammica	Lacertilia	1.90	4.81	0.41	1.75	2.45	NA	NA
Eremias multiocellata	Lacertilia	1.73	4.43	0.34	NA	NA	NA	NA
Eremiascincus fasciolatus	Lacertilia	1.61	12.50	0.65	NA	NA	NA	NA
Erythrolamprus miliaris	Lacertilia	2.01	110.05	NA	NA	NA	NA	NA
Eryx conicus	Serpentes	1.40	480.84	NA	NA	NA	NA	NA
Eryx jaculus	Serpentes	1.73	102.65	1.61	6.00	NA	3.00	24.70
Eublepharis macularius	Lacertilia	2.34	59.70	2.30	2.33	2.83	1.10	29.00
Eunectes murinus	Serpentes	1.72	5900.00	176.92	30.00	0.79	3.50	31.80
Furina ornata	Serpentes	2.00	106.94	NA	NA	NA	NA	NA
Gekko gecko	Lacertilia	2.84	63.20	2.12	2.00	4.50	1.30	23.50
Gerrhosaurus flavigularis	Lacertilia	1.96	51.71	2.33	4.75	3.00	NA	11.30
Goniurosaurus araneus	Lacertilia	1.87	22.30	1.82	2.00	2.90	NA	NA
Goniurosaurus lichtenfelderi	Lacertilia	1.85	12.40	1.21	2.00	NA	NA	NA
Goniurosaurus luii	Lacertilia	1.87	23.00	1.57	2.00	NA	NA	NA
Hemidactylus brookii	Lacertilia	3.32	2.00	0.32	2.00	2.50	NA	4.00
Hemidactylus frenatus	Lacertilia	2.44	3.30	0.22	1.99	10.70	0.60	7.00
Hemidactylus leschenaultii	Lacertilia	2.28	15.15	NA	1.50	3.00	NA	NA
Hemidactylus mabouia	Lacertilia	2.10	4.88	0.23	1.98	4.50	0.96	2.60
Hemitheconyx caudicinctus	Lacertilia	1.81	44.00	1.83	2.00	NA	1.00	16.20
Holodactylus africanus	Lacertilia	1.76	8.60	1.21	2.00	NA	NA	NA
Homalopsis buccata	Serpentes	1.82	347.20	NA	NA	NA	NA	NA
Hydrophis schistosus	Serpentes	2.75	391.37	NA	NA	NA	NA	NA
Ichnotropis capensis	Lacertilia	1.48	3.67	0.20	6.12	1.50	NA	NA
Iguana iguana	Lacertilia	2.89	1530.00	20.75	29.37	1.25	3.35	28.00
Indotyphlops braminus	Serpentes	2.98	2.07	NA	NA	NA	NA	NA
Karusasaurus polyzonus	Lacertilia	3.86	101.10	NA	2.85	1.00	NA	NA
Kentropyx calcarata	Lacertilia	1.55	24.17	0.89	4.69	1.00	NA	NA
Kentropyx paulensis	Lacertilia	1.32	10.63	NA	3.88	1.00	NA	NA
Lacerta agilis	Lacertilia	1.85	8.30	0.34	8.12	1.31	2.00	12.00
Lacerta viridis	Lacertilia	1.97	37.66	0.71	8.08	1.47	1.60	10.00
Lachesis muta	Serpentes	2.16	21669.07	NA	9.25	1.00	4.00	31.60
Lampropeltis getula	Serpentes	2.70	258.00	5.80	10.50	1.10	3.00	33.30
Latastia longicaudata	Lacertilia	1.61	14.40	0.83	6.80	NA	NA	NA
Leiolepis belliana	Lacertilia	1.65	49.99	1.64	6.00	NA	NA	5.60
Leiolepis reevesii	Lacertilia	2.20	18.60	1.22	3.70	1.50	NA	NA
Lerista desertorum	Lacertilia	1.64	3.20	0.53	NA	NA	NA	NA
Lerista frosti	Lacertilia	2.60	1.31	0.14	NA	NA	NA	NA
Lerista labialis	Lacertilia	1.73	1.13	0.15	2.00	1.50	NA	NA
Lialis burtonis	Lacertilia	2.51	18.44	3.00	1.95	1.00	NA	NA

(Continued Table S1)

Species	Suborder	Genome size	Body mass	Hatchling mass	Clutch size	Clutches per year	Age at sexual maturity	Lifespan
Liopholis inornata	Lacertilia	1.69	11.53	NA	2.06	NA	NA	NA
Mabuya mabouya	Lacertilia	1.27	12.82	0.69	4.10	1.00	NA	NA
Macrovipera lebetina	Serpentes	2.07	380.00	8.19	18.50	NA	4.00	13.30
Matobosaurus validus	Lacertilia	3.11	616.87	NA	4.00	NA	NA	17.20
Menetia greyii	Lacertilia	1.71	0.39	0.03	1.69	1.75	NA	NA
Micrurus lemniscatus	Serpentes	1.85	38.50	NA	NA	NA	NA	10.00
Mochlus sundevalli	Lacertilia	1.30	17.13	0.21	4.20	NA	NA	2.50
Morethia ruficauda	Lacertilia	1.64	0.82	0.10	NA	NA	NA	NA
Naja haje	Serpentes	2.59	2516.75	11.28	20.50	NA	NA	22.10
Naja nigricollis	Serpentes	2.66	256.70	22.31	14.00	NA	NA	23.20
Natrix maura	Serpentes	2.35	44.40	1.04	5.00	3.00	4.50	9.20
Natrix natrix	Serpentes	2.88	64.14	3.38	9.20	1.50	4.25	20.00
Natrix tessellata	Serpentes	2.00	87.50	1.39	15.00	1.00	NA	14.00
Nerodia erythrogaster	Serpentes	1.82	1442.53	6.40	17.80	1.00	NA	14.80
Nerodia sipedon	Serpentes	2.23	174.00	4.10	32.60	1.00	2.17	21.00
Opheodrys aestivus	Serpentes	1.61	17.00	1.55	10.70	1.25	2.00	7.20
Ophiodes striatus	Lacertilia	1.55	26.03	0.58	5.60	1.00	NA	NA
Ophisaurus koellikeri	Lacertilia	1.54	21.35	1.19	NA	1.00	NA	9.30
Ophisops elegans	Lacertilia	1.57	2.94	0.24	4.00	2.93	1.50	5.00
Ouroborus cataphractus	Lacertilia	3.93	58.38	NA	1.00	1.00	NA	NA
Oxyrhopus petolarius	Serpentes	1.54	34.00	3.36	NA	NA	NA	NA
Paralaudakia caucasia	Lacertilia	1.87	34.29	1.22	8.75	1.47	2.00	13.00
Paralaudakia himalayana	Lacertilia	1.97	58.87	NA	NA	NA	NA	NA
Phelsuma cepediana	Lacertilia	2.21	4.65	0.05	2.00	NA	0.90	9.30
Phelsuma ornata	Lacertilia	2.14	2.15	0.17	2.00	NA	NA	NA
Phrynocephalus helioscopus	Lacertilia	2.08	6.90	0.20	6.00	2.45	1.50	NA
Phrynocephalus versicolor	Lacertilia	1.95	3.76	0.26	2.50	1.75	NA	NA
Phrynosoma cornutum	Lacertilia	2.14	38.50	0.46	25.18	1.30	1.69	10.00
Physignathus cocincinus	Lacertilia	1.86	288.00	1.88	10.50	1.45	3.25	18.00
Platysaurus intermedius	Lacertilia	2.68	23.50	0.38	2.00	NA	NA	13.40
Platysaurus minor	Lacertilia	2.35	8.72	NA	2.00	NA	NA	NA
Podarcis melisellensis	Lacertilia	1.98	6.00	0.36	4.28	3.30	1.00	3.90
Podarcis muralis	Lacertilia	1.87	6.40	0.36	5.37	2.01	1.90	10.10
Podarcis pityusensis	Lacertilia	2.70	6.80	0.58	2.80	2.00	1.75	18.00
Podarcis tiliguerta	Lacertilia	2.25	5.00	0.45	9.00	NA	NA	15.00
Pogona vitticeps	Lacertilia	1.81	500.00	1.39	20.80	3.50	2.00	12.00
Polychrus marmoratus	Lacertilia	1.86	27.70	1.55	8.10	NA	NA	NA
Psammodromus algirus	Lacertilia	2.17	9.10	0.47	5.56	1.85	1.05	2.80
Pseudocordylus melanotus	Lacertilia	2.45	29.44	1.10	3.47	1.00	NA	NA
Pseudocordylus microlepidotus	Lacertilia	3.14	29.44	1.10	3.47	1.00	NA	2.80
Pseudopus apodus	Lacertilia	2.26	437.16	4.21	8.10	1.00	2.00	54.00
Ptyas korros	Serpentes	2.98	201.00	NA	NA	NA	NA	NA
Ptychozoon lionotum	Lacertilia	3.25	16.01	0.82	2.00	5.50	1.00	4.40
Ptyodactylus hasselquistii	Lacertilia	1.89	9.30	0.93	2.00	5.50	1.50	12.60
Python curtus	Serpentes	1.83	3454.07	NA	11.00	1.00	NA	27.80
Regina septemvittata	Serpentes	2.38	217.02	2.90	11.00	1.00	2.50	19.30
Rhabdophis subminiatus	Serpentes	1.89	135.80	NA	NA	NA	NA	NA
Saara hardwickii	Lacertilia	2.45	574.92	NA	NA	NA	NA	NA
Sceloporus magister	Lacertilia	2.73	47.50	1.73	8.23	1.73	1.65	6.00
Sceloporus occidentalis	Lacertilia	2.36	13.60	0.95	10.10	1.90	1.70	5.00
Simoselaps anomalus	Serpentes	1.81	4.49	0.63	NA	NA	NA	NA
Sinonatrix annularis	Serpentes	2.28	232.15	NA	NA	NA	NA	NA
Smaug giganteus	Lacertilia	3.36	457.04	NA	NA	NA	NA	NA
Smaug warreni	Lacertilia	3.61	130.05	NA	NA	NA	NA	NA
Stellagama stellio	Lacertilia	2.14	334.57	NA	NA	NA	NA	NA

(Continued Table S1)

Species	Suborder	Genome size	Body mass	Hatchling mass	Clutch size	Clutches per year	Age at sexual maturity	Lifespan
Takydromus sexlineatus	Lacertilia	2.40	2.20	0.16	2.20	4.50	NA	1.50
Tantilla melanocephala	Serpentes	2.25	7.00	NA	2.00	NA	NA	NA
Tarentola chazaliae	Lacertilia	1.89	10.13	NA	NA	NA	NA	NA
Tarentola delalandii	Lacertilia	2.54	9.09	0.37	1.83	7.00	NA	7.00
Tarentola mauritanica	Lacertilia	2.65	7.30	0.21	2.00	5.33	3.00	14.00
Telescopus fallax	Serpentes	2.01	53.67	NA	6.50	1.00	NA	10.00
Teratoscincus scincus	Lacertilia	2.59	22.40	1.45	1.75	2.17	0.80	13.00
Tetradactylus seps	Lacertilia	2.84	3.80	NA	NA	NA	NA	NA
Thamnophis elegans	Serpentes	2.73	377.24	1.90	8.70	1.00	NA	17.80
Thamnophis marcianus	Serpentes	2.66	90.00	2.33	19.00	1.00	1.50	7.20
Thamnophis sauritus	Serpentes	2.14	299.07	1.18	12.33	1.25	2.17	10.60
Thamnophis sirtalis	Serpentes	2.46	111.52	1.37	27.00	0.75	1.95	14.00
Thecadactylus rapicauda	Lacertilia	2.36	29.20	1.07	1.50	NA	NA	6.90
Tiliqua scincoides	Lacertilia	1.82	496.40	12.85	10.67	0.75	3.00	26.60
Timon lepidus	Lacertilia	2.35	119.80	1.44	12.74	1.30	2.50	28.00
Timon pater	Lacertilia	1.44	63.98	1.77	11.00	2.45	NA	NA
Trapelus sanguinolentus	Lacertilia	1.72	20.20	0.52	9.00	2.93	2.00	8.10
Trimeresurus albolabris	Serpentes	2.66	272.27	2.40	12.00	NA	NA	11.40
Trioceros jacksonii	Lacertilia	2.01	91.18	NA	NA	NA	NA	NA
Trogonophis wiegmanni	Lacertilia	1.65	5.70	0.41	4.25	0.68	2.50	14.00
Tropidurus torquatus	Lacertilia	2.24	21.22	0.92	5.10	2.00	0.40	3.00
Tupinambis teguixin	Lacertilia	2.61	2212.00	14.85	9.67	1.00	NA	16.10
Uma inornata	Lacertilia	2.28	56.12	NA	2.50	1.80	1.50	5.00
Uromastyx acanthinura	Lacertilia	2.19	250.40	2.80	13.00	1.30	4.50	26.00
Varanus bengalensis	Lacertilia	2.33	4940.00	9.40	20.20	1.17	2.80	22.00
Varanus exanthematicus	Lacertilia	2.06	18104.50	4.65	25.80	3.00	NA	17.00
Varanus griseus	Lacertilia	1.19	1221.50	12.08	15.80	0.66	3.50	21.00
Varanus komodoensis	Lacertilia	1.93	62070.00	84.68	19.53	1.58	6.00	62.00
Varanus niloticus	Lacertilia	2.19	2890.00	20.24	30.27	1.00	2.00	14.60
Varanus salvadorii	Lacertilia	2.29	3127.75	23.19	6.80	NA	NA	7.60
Varanus salvator	Lacertilia	2.03	4345.00	26.62	11.00	2.25	2.00	15.70
Vipera ammodytes	Serpentes	1.79	174.47	5.18	7.50	1.00	3.00	22.00
Vipera aspis	Serpentes	2.91	85.20	3.27	7.00	0.50	4.67	25.00
Vipera berus	Serpentes	2.44	74.50	3.27	8.80	0.50	3.38	19.00
Vipera eriwanensis	Serpentes	1.79	73.46	NA	NA	NA	NA	NA
Xenochrophis piscator	Serpentes	1.68	131.60	0.82	34.50	1.00	NA	9.00
Xenodon merremi	Serpentes	2.46	168.66	NA	NA	NA	NA	NA
Xerotyphlops vermicularis	Serpentes	1.96	5.45	NA	5.50	NA	NA	6.20

References for Table S1

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Table S2 Evaluation of phylogenetic signal in genome size examined.

Suborder	Blomberg's *K*		Pagel's λ			
	K	*P*-value	λ	lnLλ	lnLλ = 0 (*P*-value)	lnLλ = 1 (*P*-value)
Lacertilia	0.418	0.001	0.606	131.30	103.480 (<0.001)	111.327 (<0.001)
Serpentes	0.228	0.235	<0.001	69.814	69.814 (1.000)	59.969 (<0.001)

Note: All analyses were conducted using $\log_{10}$-transformed data. Phylogenetic signal was estimated by using Blomberg's *K* and Pagel's λ. *K* and λ of 1 are indicative of genome size evolution following a Brownian motion model. For Blomberg's *K*, significant *P*-values show phylogenetic signal in the genome size. For Pagel's λ, the maximum likelihood estimate of λ was compared using likelihood ratio test to models were $\lambda = 0$ and $\lambda = 1$, respectively. Significant P-values show if λ differs significantly from models assuming no phylogenetic signal ($\lambda = 0$) or strong phylogenetic signal ($\lambda = 1$).

Table S3 Comparison of model parameters and fit for each suborder examined under Brownian motion, Ornstein-Uhlenbeck and Early-burst evolutionary models.

Suborder	Brownian motion model					Ornstein–Uhlenbeck model					Early burst model				
	σ^2	lnL	AICc	Δ_i	ω_i	α	lnL	AICc	Δ_i	ω_i	a	lnL	AICc	Δ_i	ω_i
Lacertilia	2.0^{-4}	111.33	–218.56	23.63	7.40^{-6}	0.01	124.19	–242.19	0.00	1.00	-1.00^{-6}	111.33	–216.46	25.73	2.59^{-6}
Serpentes	3.0^{-4}	59.97	–115.76	20.21	4.09^{-5}	0.06	71.16	–135.97	0.00	1.00	-1.00^{-6}	–59.97	–113.58	22.39	1.37^{-5}

Note: The Brownian rate parameter, σ^2, and rate of evolutionary change parameter, *a*, are presented for the BM, and EB models, respectively. For all models the maximum likelihood estimates (lnL) and sample size corrected Akaike Information Criterion (AICc) values are presented. To compare model fits, for each suborder we report the value of delta AICc, Δ_i, and the Akaike weights, ω_i, which indicate the strength of evidence for each model.

Table S4 Associations between body mass and life histories for the two suborders in squamata using phylogenetic generalized least squares models. Phylogenetic scaling parameters (superscripts following λ denote *P*-values of likelihood ratio tests against models with $\lambda = 0$ and $\lambda = 1$, respectively).

Suborder	Predictors	Body mass				
		λ	β	*t*	R^2	*P*
Serpentes	Hatchling mass	$<0.001^{1,<0.001}$	0.666	4.630	0.573	<0.001
	Clutch size		0.979	2.999	0.360	0.009
	Clutches per year		0.229	0.640	0.025	0.531
	Age at sexual maturity		0.355	0.623	0.024	0.542
	Lifespan		0.416	1.222	0.085	0.239
Lacertilia	Hatchling mass	$<0.001^{1,<0.001}$	1.186	15.999	0.850	<0.001
	Clutch size		0.978	7.001	0.522	<0.001
	Clutches per year		0.854	4.923	0.139	<0.001
	Age at sexual maturity		–0.016	–0.079	0.085	0.937
	Lifespan		0.415	2.953	0.017	0.005

Table S5 Associations between genome size and life histories in squamata using phylogenetic generalized least squares models. Phylogenetic scaling parameters (superscripts following λ denote *P*-values of likelihood ratio tests against models with $\lambda = 0$ and $\lambda = 1$, respectively).

Suborder	Predictors	Genome size				
		λ	β	*t*	R^2	*P*
Serpentes	Body mass	$<0.001^{1,0.123}$	0.201	0.469	0.006	0.642
	Hatchling mass		–0.038	–0.791	0.017	0.434
	Clutch size		–0.012	–0.155	<0.001	0.878
Lacertilia	Body mass	$0.246^{0.475,<0.001}$	0.021	0.510	0.005	0.612
	Hatchling mass		–0.020	–0.359	0.002	0.721
	Clutch size		–0.054	–0.864	0.013	0.391
	Clutches per year		–0.045	–0.680	0.009	0.500
	Lifespan		–0.006	–0.153	<0.001	0.879