

Evolution of North American Lizards

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Lizards are a diverse reptile group with an ancient and global evolutionary history. Fossil lizards first appeared in North America during the Mesozoic. Many lizard lineages have inhabited North America throughout geologic time, including several lineages that are extinct, others that no longer occur on the continent, and many groups that are still there today. Lizards are currently found in a diverse range of habitats and in regions across the continent, including islands and human-modified habitats. The modern lizard biota of North America contains diverse biogeographic and phylogenetic components along with the evolution of many distinctive behaviours, morphologies, and ecologies, including the evolution of venom, repeated limb loss, and ecological specialisations. Some lizards have been introduced to North America from elsewhere in the world or the continent, posing a potential problem for native biodiversity.

Introduction

Squamata (lizards and snakes) is a diverse, extant reptile clade united by many skeletal and soft tissue synapomorphies (Estes *et al.*, 1988; Simões *et al.*, 2018). Total clade Squamata is an ancient radiation thought to have originated during the late Triassic Period (Simões *et al.*, 2018). ‘Lizards’ are an evolutionary grade considered here to include all squamates besides snakes.

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Thus, no synapomorphy or suite of synapomorphies diagnoses lizards to the exclusion of all other animals. **See also: Serpentes (Snakes)**. However, most lizards share the same body plan, having four limbs, ear openings, relatively kinetic skulls compared to non-squamate reptiles, and symmetrical lungs, although limblessness and accompanying morphological adaptations evolved independently in several lineages. **See also: Sauria (Lizards)**. Lizards are familiar components of the ecosystems they inhabit and are frequent subjects of scientific research, including conservation (Diele-Viegas *et al.*, 2020), behaviour (McElroy, 2019), phylogenetics (Burbrink *et al.*, 2019a; Simões *et al.*, 2018), biodiversity (Wiens *et al.*, 2013), and ecomorphology (Sherratt *et al.*, 2015). Here, we focus on the evolution of extant and extinct lizards from North America, including the United States, Canada, Mexico, Central America and the Caribbean.

Currently, there are well over 700 native lizard species in North America representing many extant lineages (**Figure 1**) (iNaturalist, 2020). However, the continent was once populated by several lineages that are now extinct (e.g. polyglyphanodontians), and some extant lineages were fully extirpated at some point in the past (e.g. varanids). Additionally, many taxa with a long evolutionary history on the continent have experienced substantial biogeographic shifts and ecological changes, while other groups have remained relatively stable through geologic time.

In the modern biota, pleurodontan iguanians (**Figure 2**) are exceptionally diverse, particularly phrynosomatids (horned lizards, spiny lizards, and relatives) and dactyloids (anoles). Skinks, geckos, anguids (alligator and glass lizards, galliwasp), teiids (whiptails and relatives), and gymnophthalmids (spectacled lizards) (**Figure 3b–e**) are also well-represented (**Table 1**). Morphologically and behaviourally distinctive groups include helodermatids (gila monsters) (**Figure 3a**), xantusiids (night lizards) (**Figure 3f**), xenosaurids (knob-scaled lizards), and amphisbaenians (worm lizards). North American lizards range in size from tiny *Sphaerodactylus* geckos (~2 cm) to massive *Iguana* (>1 m) and can be found in all habitats and regions besides the colder and northern portions of the continent. The

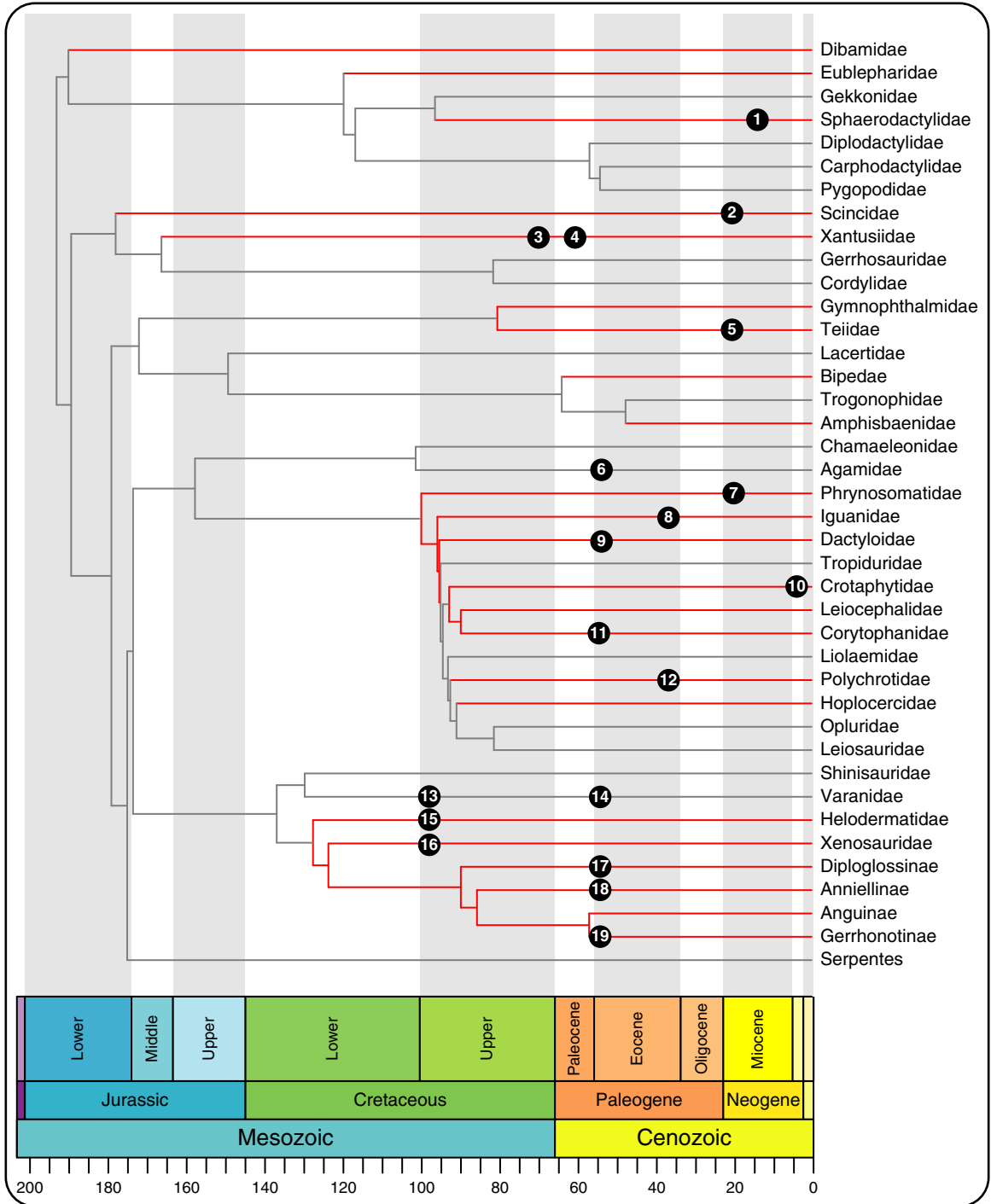


Figure 1 Timetree of Squamata derived from Burbrink *et al.* (2019a,2019b) showing most major clades. Phyllodactylidae, Alopoglossidae, Rhineuridae, Blanidae and Cadeidae were not included in the analysis of Burbrink *et al.* (2019a) and were not attached to the tree *post hoc*. For convenience and consistency, most lineages are shown at the level of monophyletic families; for anguids, subfamilies are shown instead. Lizard lineages that are found in North America in the modern biota are denoted with red branches, and those that do not currently inhabit North America and snakes have grey branches. Numbered circles represent, to our knowledge, the first reported fossil of a given clade in North America. A fossil is not assigned to every lineage. Note that fossils are not necessarily part of the crown clade of the lineage to which they are assigned, the referrals of some fossils to a given clade are explicitly tentative, and no fossils besides *Paleoxantusia* were used to calibrate the tree from Burbrink *et al.* (2019a). The tree was produced using the package 'strap' (Bell and Lloyd, 2015) in RStudio (RStudio Team, 2016). The yellow box to the right of 'Neogene' indicates the Quaternary, the box to the right of 'Miocene' indicates the Pliocene, and the box to the right of the Pliocene indicates the Pleistocene. **1.** *Sphaerodactylus* (Wang and Xing, 2020). **2.** Putative skinks (Estes, 1983). **3.** Putative xantusiid (*Catactegenys solaster*, see Nydam, 2013). **4.** *Paleoxantusia* (see Estes, 1983). **5.** Putative teiids (Estes, 1983). **6.** *Tinosaurus* (Smith and Gauthier, 2013). **7.** Indeterminate phrynosomatids (Chovanec, 2014). **8.** *Queironius praelapsus* (Smith, 2011). **9.** *Paranolis delicatus* (Smith, 2009). **10.** Fossil crotaphytids (Hollenshead and Mead, 2006). **11.** *Suzaniwanna patriciana* (Smith, 2009). **12.** *Sauropithecooides charisticus* (Smith, 2011). **13.** Potential varanid (*Palaeosaniwa canadensis*, see Nydam, 2013). **14.** *Saniwa* (Smith and Gauthier, 2013). **15.** Potential helodermatid (*Primaderma nessovi*, see Nydam, 2013). **16.** New xenosaurid (see Nydam, 2013). **17.** Indeterminate diploglossine fossils (Smith, 2009). **18.** *Apodosauriscus thermophilus* (Smith, 2009). **19.** Indeterminate gerrhonotine fossils (Smith, 2009). Burbrink FT, Grazziotin FG, Pyron RA, et al. (2019a) Interrogating genomic-scale data for Squamata (lizards, snakes, and amphisbaenians) shows no support for key traditional morphological relationships. *Systematic Biology* 69: 502–520. <https://doi.org/10.1093/sysbio/syz062>; Burbrink FT, Grazziotin FG, Pyron RA, et al. (2019b) Data from: Interrogating genomic-scale data for Squamata (lizards, snakes, and amphisbaenians) shows no support for key traditional morphological relationships. Dryad Digital Repository. <https://doi.org/10.5061/DRYAD.SM6JB0P>; Bell and Lloyd, 2015; RStudio Team, 2016.

extant North American lizard biota contains diverse biogeographic components (Figure 4). Extant North American lizards exhibit a broad range of morphologies (Figures 2 and 3) and a correspondingly wide array of life histories, including taxa that are terrestrial (e.g. teiids), arboreal (e.g. *Sceloporus*, *Abronia*), fossorial (amphisbaenians, *Anniella*), semi-aquatic (several species of *Anolis*), and saxicolous (e.g. *Xenosaurus*) (Figure 5).

Spatiotemporal Evolution of North American Lizards

The fossil record

Fossil Lizards

The lizard skull is largely held together by soft tissue connections between bones (Evans, 2008). As a result, a majority of fossil lizards are only known from disarticulated and often isolated skeletal elements. In addition, the typical small size of lizard bones reduces their likelihood of being preserved as fossils, and when they are fossilised, they may be fragmented (Evans, 2003). These factors can result in difficulties in identifying fossil lizards, and palaeontologists must rely on an understanding of patterns of skeletal variation in living lizards in order to contextualise lizards of the past (Bell and Mead, 2014). The fragmented and incomplete nature of the fossil record can exacerbate differences among phylogenetic and biogeographic hypotheses inferred from morphological or molecular data. Thus, it is important to evaluate information from multiple data sources to elucidate the evolutionary history of North American lizards.

Mesozoic

The earliest lizard fossils recovered from North America are from the late Jurassic, postdating the breakup of Pangea. These fossils include extinct anguimorph and scincoidean lizards, like dorsetisaurids and paramacellodids (Evans, 2003; Nydam, 2013). Fossil lizards from the early Cretaceous in North America are scarce, although there are some stem squamates from central Mexico (Nydam, 2013). North American fossil lizards become

increasingly abundant during the middle and Late Cretaceous. Notably, the first known fossil of a lizard referred to the extant family Helodermatidae appears during the middle Cretaceous (Evans, 2003). During the Late Cretaceous, the extinct polyglyphanodontians are known from North American deposits, as are xantusiid-like contogeniids (Nydam, 2013). The earliest anguids appear in Late Cretaceous strata (Nydam, 2013) as did iguanians (DeMar *et al.*, 2017) and tentatively identified pleurodontan (=Iguanidae sensu Macey *et al.*, 1997) fossils (Longrich *et al.*, 2012; Nydam, 2013). Many anguimorphs and fossils tentatively referred to Xantusiidae and Xenosauridae are also known from the Late Cretaceous of North America (Nydam, 2013). One notable group that appeared in the Late Cretaceous is the mosasaurs, an extinct group of marine squamates (Polcyn *et al.*, 2014). Mosasaurs went extinct at the end of the Cretaceous, as did polyglyphanodontians (Nydam, 2013).

Paleogene

Contogeniids, xenosaurids, anguids, non-anguid anguimorphs and probably pleurodontans persisted after the end-Cretaceous extinction (Longrich *et al.*, 2012). The large and heavily armoured glyptosaurines (Anguidae) are well-documented across the continent, and xantusiids and anguimorphs are common in Paleocene deposits in the western and central United States (Estes, 1983).

Many extant family-level clades appear during the Eocene, although not necessarily in the areas in which they occur today. Middle latitude faunas included taxa that are now found largely in the tropics or subtropics, such as corytophanids, dactyloids, polychrotids, diploglossines and xantusiids, as well as taxa that were later extirpated from North America, like acrodontan iguanians and varanids (Smith, 2009, 2011; Smith and Gauthier, 2013). Gerrhonotines were present in middle latitudes during the Eocene (Smith, 2009), around the time of the hypothesized divergence between gerrhonotines and anguines (Figure 1).

Glyptosaurines are relatively common in Oligocene strata, as are xantusiids, amphisbaenians and systematically enigmatic pleurodontans (e.g. *Parasauromalus*, *Aciprion*). Even though the climate was less equable than during much of the Eocene, diverse lizard assemblages were found further north than they are today,



Figure 2 Extant diversity of pleurodantan lizards in North America. (a) *Enyalioides heterolepis*, a wood-lizard found in Panama and one of the few hoplocercids currently found in North America. Image by B. White. (b) *Phrynosoma cornutum*, a phrynosomatid lizard known for its head horns. Image by S. Scarpetta. (c) *Cophosaurus texanus*, a phrynosomatid lizard found in the southwestern United States and northern Mexico, displaying breeding colours on the side of its body. Image by B. White. (d) *Anolis desiradei*, an anole restricted to the island of Desirade in the Lesser Antilles. Image by S. Scarpetta. (e) *Crotaphytus reticulatus*, a particularly large crotaphytid lizard found in southern Texas and northwestern Mexico that is notable for being the only species of *Crotaphytus* that is not associated with rocky habitats, and that is displaying its gular fold. Image by Drew R. Davis.

such as in the Cypress Hills Formation in Saskatchewan (Holman, 1972). The extinction of glyptosaurines probably occurred during the middle or late Oligocene (Scarpetta, 2019a).

Neogene

Cooling and aridification in the later Eocene and the Oligocene appears to have caused extinctions, migrations, and local extirpations at the community and larger clade level (Scarpetta, 2019a).

Accordingly, taxa occurring in the early Cenozoic seem to have been replaced by a more modern assemblage during the late Paleogene and early Neogene. The earliest records of several extant genus-level clades occur during the Miocene, such as the alligator lizard *Elgaria* (Scarpetta, 2018) and the fringe-toed lizard *Uma* (Scarpetta, 2019b), although those taxa did not necessarily inhabit the same ecosystems as they do today. Total clade phrynosomatids are thought to have a long evolutionary



Figure 3 Extant lizard diversity in North America. (a) *Heloderma suspectum*, a venomous lizard found in the southern United States and northern Mexico. Image by B. White. (b) *Plestiodon obsoletus*, a large-bodied skink found in the Great Plains region and in the southwestern United States and northern Mexico. Image by Drew R. Davis. (c) *Coleonyx elegans*, a eublepharid gecko, a group known for lacking toepads and for possessing movable eyelids. (d) *Sphaerodactylus glaucus*, a gecko that is one of the smallest lizards in the world. (e) *Holcosus gaigeae*, a teiid lizard from northeastern Yucatán Peninsula. (f) *Lepidophyma flavimaculatum*, a tropical night lizard found throughout central America. (c–f) Image by B. White.

history extending into the middle Cretaceous (**Figure 1**), but there are few fossils assigned unambiguously to Phrynosomatidae (Chovanec, 2014). Similarly, unambiguous fossil crotaphytids are not reported until the Neogene (Hollenshead and Mead, 2006) but Crotaphytidae is hypothesised to have diverged from corytophanids and leiocephalids during the Cretaceous.

Fossil lizards referred to Teiidae are reported from the early Miocene onwards (Estes, 1983), but the identifications of most of

those fossils are tenuous given their fragmentary nature and historical problems with teiid phylogeny (Barley *et al.*, 2019; Scarpetta, 2020). Fossil lizards that resemble modern North American skinks are known from the Miocene in the eastern and central United States, and more putative fossil skinks are described from the Oligocene (Estes, 1983).

Geckos fossilise poorly due to the generally fragile nature of their skeletons, but several *Sphaerodactylus* are preserved

Table 1 Diversity of extant lizards in North America.

More inclusive clade	Family and/or Subfamily level clade	Genera
Pleurodonta	Phrynosomatidae	<i>Phrynosoma</i> , <i>Uma</i> , <i>Callisaurus</i> , <i>Cophosaurus</i> , <i>Holbrookia</i> , <i>Sceloporus</i> , <i>Uta</i> , <i>Urosaurus</i> , <i>Petrosaurus</i>
Pleurodonta	Crotaphytidae	<i>Crotaphytus</i> , <i>Gambelia</i>
Pleurodonta	Iguanidae	<i>Dipsosaurus</i> , <i>Sauromalus</i> , <i>Iguana</i> , <i>Cyclura</i>
Pleurodonta	Dactyloidae	<i>Anolis</i>
Pleurodonta	Corytophanidae	<i>Basiliscus</i> , <i>Laemanctus</i> , <i>Corytophanes</i>
Pleurodonta	Leiocephalidae	<i>Leiocephalus</i>
Pleurodonta	Polychrotidae	<i>Polychrus</i>
Pleurodonta	Hoploceroidae	<i>Enyalioides</i>
Teiioidea	Teiidae	<i>Aspidoscelis</i> , <i>Holcosus</i> , <i>Pholidoscelis</i> , <i>Ameiva</i> , <i>Cnemidophorus</i>
Teiioidea	Gymnophthalmidae	<i>Gymnophthalmus</i> , <i>Loxopholis</i> , <i>Anadia</i> , <i>Echinosaura</i> , <i>Bachia</i> , <i>Tretioscincus</i>
Teiioidea	Alopoglossidae	<i>Ptychoglossus</i>
Amphisbaenia ^a	Rhineuridae	<i>Rhineura</i>
Amphisbaenia	Bipedidae	<i>Bipes</i>
Amphisbaenia	Amphisbaenidae	<i>Amphisbaena</i>
Amphisbaenia	Cadeidae	<i>Cadea</i>
Scincomorpha	Scincidae	<i>Plestiodon</i> , <i>Scincella</i> , <i>Mabuya</i>
Scincomorpha	Xantusiidae	<i>Xantusia</i> , <i>Lepidophyma</i> , <i>Cricosaura</i>
Anguimorpha	Gerrhonotinae (Anguidae)	<i>Elgaria</i> , <i>Gerrhonotus</i> , <i>Barisia</i> , <i>Mesaspis</i> , <i>Abronia</i>
Anguimorpha	Anguinae (Anguidae)	<i>Ophisaurus</i>
Anguimorpha	Diploglossinae (Anguidae)	<i>Diploglossus</i> , <i>Celestus</i>
Anguimorpha	Annielinae (Anguidae)	<i>Anniella</i>
Anguimorpha	Xenosauridae	<i>Xenosaurus</i>
Anguimorpha	Helodermatidae	<i>Heloderma</i>
Gekkota	Eublepharidae	<i>Coleonyx</i>
Gekkota	Phyllodactylidae	<i>Phyllodactylus</i>
Gekkota	Sphaerodactylidae	<i>Sphaerodactylus</i> , <i>Aristelliger</i>

^aNext to Rhineuridae denotes that there is ambiguity about the phylogenetic position of that clade with respect to other amphisbaenians, given the results of Streicher and Wiens (2017).

in Miocene amber from the Dominican Republic (Wang and Xing, 2020). Fossil *Anolis* are preserved in amber from Mexico and Hispaniola, the latter of which are hypothesised to indicate long-term ecomorphological stability of Caribbean *Anolis* communities since the early or middle Miocene (Sherratt *et al.*, 2015; Wang and Xing, 2020).

Quaternary

There is a robust fossil record of lizards from the Quaternary (Pleistocene and Holocene epochs). The Quaternary represents a time period with a dynamic history of environmental change, including numerous glacial and interglacial cycles and changes in landscapes. Quaternary lizards from the mainland (north of Mexico) were hypothesised to have been taxonomically and geographically stable during much of the Quaternary because there were few documented extinct taxa, and identified fossils were representative of modern species that live in the region today (reviewed by Holman, 1995). It was later argued that this hypothesis was founded on biased fossil identification practices (Bell *et al.*, 2010). Other researchers have argued for significant range

shifts in lizard taxa (e.g. Hutchison *et al.*, 1999) and potential lineage diversification during the Pleistocene (e.g. Gottscho *et al.*, 2017; Scarpetta, 2019b).

Several lizards went extinct during the Quaternary in North America with most of these extinctions occurring in the Caribbean during the more recent Holocene epoch (Slavenko *et al.*, 2016; Bochaton *et al.*, 2017). Extirpation of lizards from Caribbean islands is documented (e.g. Bochaton *et al.*, 2016; Kemp and Hadly, 2015, 2016) and human actions were hypothesised to have played a significant role in shaping several of these island lizard communities (Bochaton *et al.*, 2017). Continued, modern, human-mediated environmental changes during the Quaternary, including climate change, will continue to impact extant lizard populations (Diele-Viegas *et al.*, 2020).

Biogeography

Mainland North America

There is some debate about the historic biogeographic origins of lizards in North America. However, fossil and molecular evidence suggests various vicariance and dispersal scenarios for different clades that led to their extant ranges. Previous research suggested

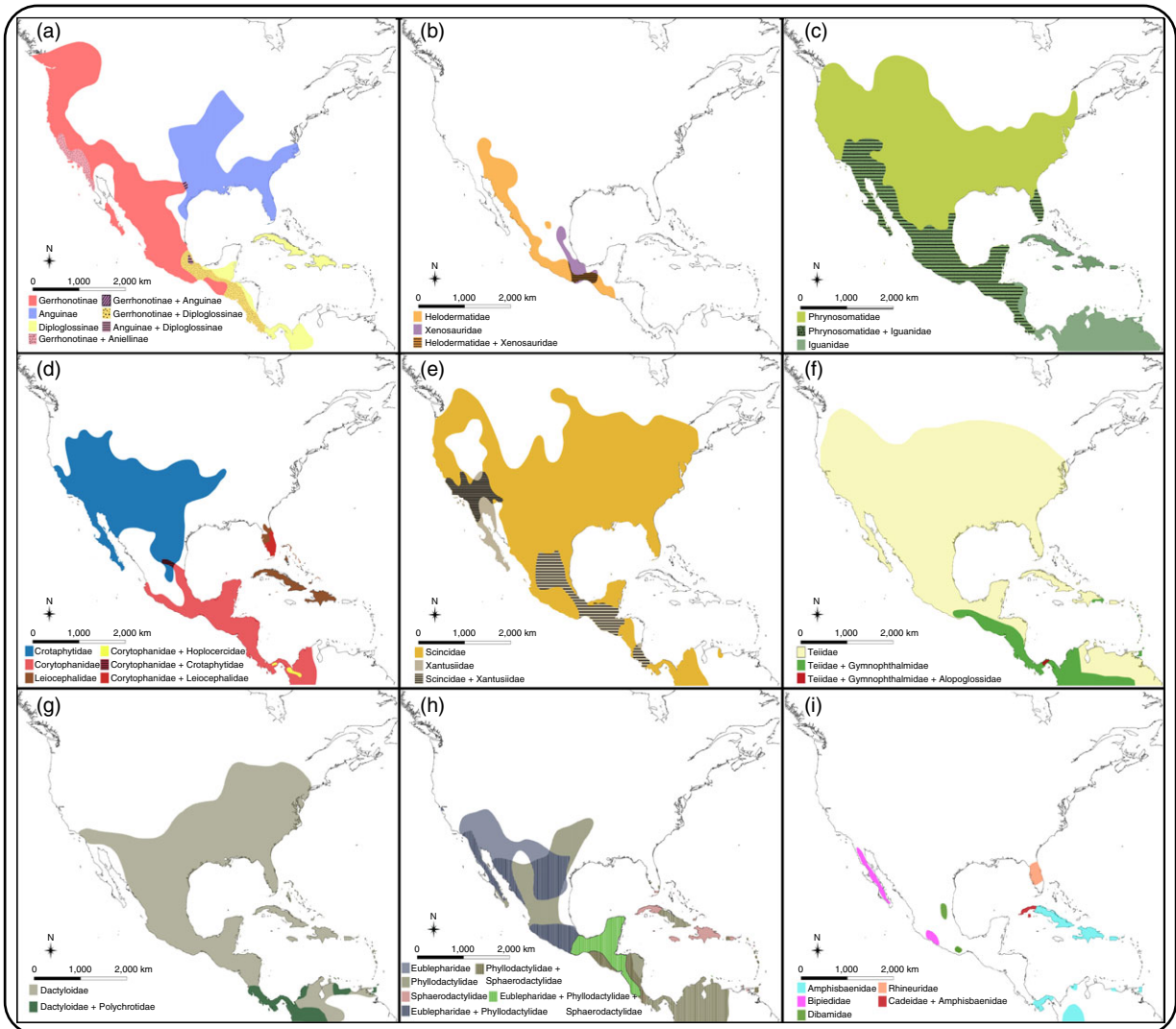


Figure 4 Extant geographic distributions of lizards in North America. (a) Gerrhonotinae, Anguinae, Aniellinae, and Diploglossinae. (b) Helodermatidae and Xenosauridae. (c) Phrynosomatidae and Iguanidae. (d) Crotophytidae, Corytophanidae, Leiocephalidae, and Hoplocercidae. (e) Scincidae and Xantusiidae. (f) Teiidae, Gymnophthalmidae, and Alopoglossidae. (g) Dactyloidae and Polychrotidae. (h). Eublepharidae, Phyllodactylidae, and Sphaerodactylidae. (i) Amphisbaenidae, Bipedidae, Dibamidae, and Cadeidae. GBIF.org (2020) GBIF Occurrence Download <https://doi.org/10.15468/dl.m7tmxs>. Accessed 20 May, 2020.

a North American origin for pleurodontans and a subsequent dispersal into Central and South America (Townsend *et al.*, 2011). This stood in stark contrast to the previous view of pleurodontans arising through a South American origin. Pleurodontans are now widespread and found as far north as the northeast United States and southern Canada down through Mexico and Central America (**Figure 4**). Anguinae is another widely distributed lizard clade that is thought to have a Laurasian origin (Macey *et al.*, 1999). Vicariance events resulting from the formation of mountain ranges and climatic shifts in North America then led to further splitting of anguids, including the subfamily Gerrhonotinae (Macey *et al.*, 1999). Gerrhonotines are primarily found in western and southern North America, but several genera reside in

the tropical regions of Mexico and Central America. *Ophisaurus*, commonly known as the glass lizards, are hypothesised to have colonised North America from Asia via the Bering land bridge (Macey *et al.*, 1999).

Skinks likely dispersed to North America via the Bering land bridge before radiating south into their modern range (Macey *et al.*, 2006) (**Figure 4**). Eublepharid geckos likely colonised in a similar manner, aided by a warming of the North American climate during the Paleocene and part of the Eocene (Gamble *et al.*, 2011). Molecular data coupled with geomorphology provides evidence for lineage diversification in *Coleonyx* (Leavitt *et al.*, 2020) and *Urosaurus* (Feldman *et al.*, 2011) that is associated with the formation of the Baja California Peninsula. Similarly,

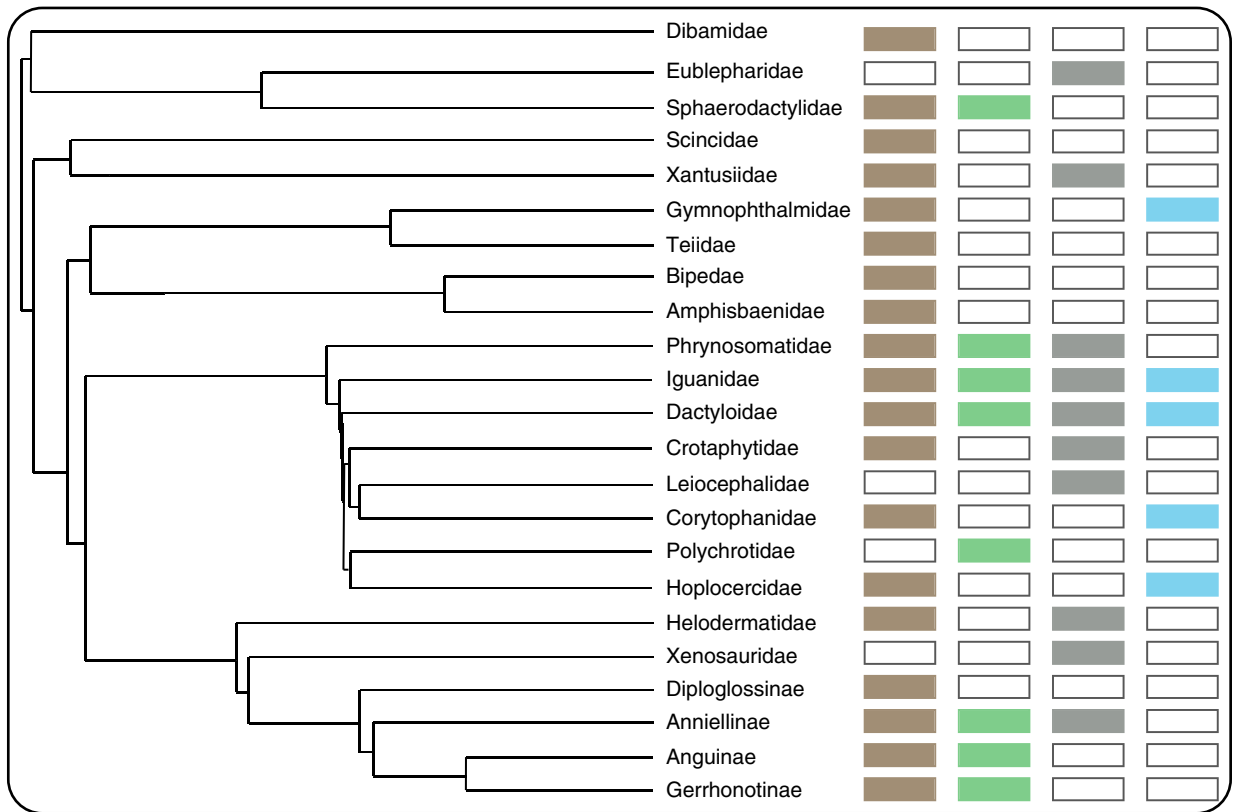


Figure 5 Ecological microhabitat modes of North American lizards. The phylogeny contains only taxa currently found in North America. Terrestrial and/or fossorial is in brown, arboreal is in green, saxicolous is in grey, and semi-aquatic is in blue. Adapted from Blankers T, Townsend TM, Pepe K, *et al.* (2013) Contrasting global-scale evolutionary radiations: Phylogeny, diversification, and morphological evolution in the major clades of iguanian lizards. *Biological Journal of the Linnean Society* 108: 127–143. <https://doi.org/10.1111/j.1095-8312.2012.01988.x>.

vicariant lineage diversification in some *Plestiodon* may have resulted from the formation of the Trans-Mexican Volcanic Belt (Pavón-Vázquez *et al.*, 2018). Migration around mountains in nuclear Central America is hypothesised to have caused diversification in some mainland *Anolis* (Gray *et al.*, 2019). A phylogenetic and biogeographic analysis of *Anolis* inferred a faunal exchange through the Isthmus of Panama during the Miocene (Poe *et al.*, 2017).

Biogeographic hypotheses often change as new fossil and molecular evidence comes to light. See also: **History of Biogeography**. However, the overall pattern of lizard colonisation in North America suggests various scenarios of dispersal from Asian regions, coupled with vicariance on the ancient landmass of Laurasia that would eventually become the North America we see today. In addition, clades continued to diversify and expand their ranges south into Central and South America. For example, polychrotids and hoplocercids spread into South America but appear to have later recolonised Central America (Figure 4).

Caribbean

Oversea dispersal from Central and South America is often regarded as the principal method of origin for most Caribbean herpetofaunas, with both biological and geological evidence

rendering other hypotheses of vicariance and historical land bridges unlikely (Tucker *et al.*, 2017). An emerging pattern of biogeographic scenarios in lizard appearances has been a southeast to northwest colonisation beginning in either South or Central America, aided by the proximity of islands to these landmasses and ocean currents travelling in such a direction up the archipelago. Evidence suggests that many lizards (e.g. *Pholidoscelis*, *Anolis*, and *Cyclura*) have followed this colonisation pattern (Tucker *et al.*, 2017; Losos, 2009; Malone *et al.*, 2000). This may explain why family-level lizard clades are often widespread across various islands, even in cases of high endemism on individual islands. Other lizards such as *Diploglossus* and *Leiocephalus* appear to have a North American origin (Macey *et al.*, 1999; Hedges, 1996). Geckos were successful in colonising the Caribbean as well, and evidence suggests multiple dispersal events of geckos as recent as the Quaternary (Hedges, 1996). Most lizards probably arrived on flotsam or other floating debris, although there is evidence of dispersal by hurricanes between islands in close proximity (Hedges, 1996; Censky *et al.*, 1998).

Today, lizards are found on most Caribbean islands and in a diverse array of habitats. *Anolis* (Figure 2d) in particular have been highly successful in colonising a wide range of ecological

niches in the Greater Antilles following their initial arrival to the Caribbean in the second half of the Cenozoic (Losos, 2009). Iguanidae is also widespread, with the genus *Cyclura* occupying roughly 12 different islands across the Greater Antilles since their hypothesised arrival in the Miocene (Malone *et al.*, 2000). Notably, these iguanas have since been extirpated from much of their historic range and inhabit severely degraded areas of habitats. This pattern of reduced habitat and range is seen in many other lizards. *Iguana delicatissima* was once the only iguana in the Lesser Antilles but has since seen an invasion of its range by its relative *Iguana iguana*, which is native to other parts of the Caribbean (Hedges, 1996). Skinks (*Mabuya*) are found throughout the Greater and Lesser Antilles as well (Miralles *et al.*, 2009). Notably, no skinks are found in Cuba, possibly because it is a difficult island to reach by flotsam, or because skinks were eradicated on the island by humans and introduced predators (Hedges and Conn, 2012).

Ecological Diversification

North American lizards are characterised by the evolution of behavioural, morphological, and ecological diversity. Here we provide a brief overview of that spectacular diversity.

Behavioural

Lizard colouration provides an approximation of their behaviour. In general, lizards are primarily cryptic and inconspicuously coloured, allowing them to remain hidden in plain sight. However, this is not the rule. The venomous genus, *Heloderma*, may represent one of the few true examples of aposematic warning colouration in lizards (McElroy, 2019). Pale pink-orange splotches abut stark black lines in *Heloderma suspectum* (Figure 3a), presumably functioning similarly to the predator repellent colours of poison dart frogs or the warning colouration in coral snakes. Largely, the use of eye-catching colouration to warn of poisonousness or venomousness are few in lizards. Bluetail colouration in some skinks and teiids, such as *Plestiodon obsoletus* or *Aspidoscelis ornatus*, is common in juveniles. In lacerterids, this type of colouration is associated with risky behaviour and the use of open microhabitat (Hawlena, 2009). Colour is further employed as a pursuit deterrent signal in *Cophosaurus texanus* and *Callisaurus draconoides* (Figure 2c), which wave banded tails at predators, and in some *Anolis*, dewlap extension is used to deter potential predators (Losos, 2009). In fact, much of the current literature on lizard behaviour focuses on bright throats or dorsal breeding colouration in males (Losos, 2009; Leaché *et al.*, 2014), but few studies have examined the interplay of evolutionary and ecological drivers behind female colour, colour differences between the sexes, and biogeographic colour variation (White *et al.*, 2019).

Morphological

Morphological variation in lizards includes an array of predation defences, body size dimorphisms, and, thus, ecologies. For instance, horn number distinguishes species and serves as an

adaptive defence in the radiation of *Phrynosoma* (Luxbacher and Knouft, 2009). Other morphological peculiarities that may provide protection include the osteoderms in anguids (Figure 2b), tail spines in *Ctenosaura* used to block entrances, and body cavity inflation in *Sauromalus* to prevent extraction by predators. Of course, not all North American lizard morphological variation can be summarised by competitive interactions with heterospecifics. Geckos have crepuscular and/or nocturnal life histories that seem to require vision, toe pad, and tail modifications (Figure 3c,d; Underwood, 1954). Examination of the limb-reduced amphisbaenids reveals a reduced right lung, contrasting with other legless lizards and snakes that have a reduced left lung (Lynn and Komorowski, 1957). Limb loss or reduction has evolved in multiple North American lizard lineages, including other amphisbaenians, the skink *Plestiodon reynoldsi*, the gymnophthalmid *Bachia*, and the anguid *Ophisaurus*.

Ecological

In more northern latitudes, niche space is largely filled by phrynosomatids and relatively few other pleurodontans are represented (Blankers *et al.*, 2013). Still, specialists such as carnivorous, lizard-eating *Gambelia*, insectivorous *Phrynosoma*, and herbivorous desert iguanas (*Dipsosaurus*) co-occur in Baja California and the western US, while many of the major pleurodontan lineages partition microhabitats sympatrically in Central America. The role of competitive interactions on morphological diversification is well-studied in *Anolis*. Across the Antillean islands, anoles present a simplified and repeated natural experiment of ecological outcomes. In summary, competitive interactions between anoles can predict foraging mode, microhabitat use, and ultimately, body size (Losos, 2009). For instance, body size reinforces niche partitioning between larger anoles that may prey upon smaller anoles. In addition to competitive interactions, historical climatic variation has been found to influence body size evolution in this group (Velasco *et al.*, 2020). To generalise, Antillean anoles can be thought of as a simplified system that provides some understanding of the ecological influences acting on lizard diversity and thus, given the size and array of habitat availability in North America the diversity in lizard ecologies is no surprise (Figure 5).

Niche Space in the Modern Era and Introduced Species

Introduced species are most prevalent in subtropical and tropical port towns where trade is popular. Introductions of non-native species by humans have altered biogeography and ecosystem functioning in North America (Ellis, 2015). In the Caribbean, biogeography has been altered fundamentally by introductions of species historically for food (Kemp *et al.*, 2020), via cargo shipments (Helmus *et al.*, 2014), and in the modern era, the pet and nursery trades are increasing establishment opportunities (Bomford *et al.*, 2009). Most species introduced to areas outside of their natural range fail to persist to invasive status. Those that do are typically from climatic regions that are similar to the conditions of the introduction site and therefore are

well-suited to those conditions (Case and Bolger, 1991; Bomford *et al.*, 2009; Kemp *et al.*, 2020). Notable standouts include *Anolis sagrei*, *Hemidactylus frenatus*, and *Hemidactylus turcicus*, all of which are dispersed widely in the southern United States and much of Central America. It has been hypothesised that these animals may outcompete native species for resources, but invasive species tend to be generalists that excel in depauperate, urbanised habitats (Francis and Chadwick, 2015; McKinney, 2006; Wright, 2009). **See also: Invasion of Introduced Species.** However, introduced lizards can present serious conservation concerns. In Florida, Argentine tegus alter ecosystem function through potential changes in native seed dispersal and predation of native alligator and turtle nests (Jarnevich *et al.*, 2018). Responsible pet ownership, regulation of trade, and prevention measures reduce these intractable situations and reframe the focus of biodiversity loss to more immediate conservation concerns of habitat loss and climate change.

Final Remarks

The evolutionary history of lizards in North America spans the Jurassic period to the present. Several lineages that once inhabited the continent now are extinct, and others have been extirpated from the North American landmass. The modern biota contains many extant lineages and is characterised by both cosmopolitan and endemic clades. Accordingly, extant lizards throughout North America exhibit a wide variety of morphologies and have been successful in colonising almost all habitats, including human-modified habitats.

There are some aspects of North American lizard evolution that require more attention. Patterns of skeletal variation in most extant lizard species are poorly understood (Bell and Mead, 2014), hindering our capacity to interpret the fossil record. We are far from understanding the full diversity of lizards that have inhabited the continent through geologic time. For many North American lizards but for pleurodontans, in particular, molecular divergence times substantially predate the known fossil record, creating some discordance among biogeographic and phylogenetic hypotheses based primarily on either data type (e.g. compare DeMar *et al.*, 2017 with Townsend *et al.*, 2011). Although next-generation sequencing has illuminated the relationships among many extant species (e.g. Burbrink *et al.*, 2019a), the phylogenetic relationships of some extant groups (e.g. amphisbaenians, the interrelationships of some pleurodontans) and many taxa known only from fossils (e.g. mosasaurs and many other Mesozoic squamates) remain unresolved. Finally, the evolutionary and ecological processes leading or not leading to morphological adaptation continue to confound researchers.

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Glossary

- Clade** A monophyletic group, that is, a group that contains an ancestor and all of its descendants.
- Crown clade** The clade containing all extant representatives of a clade, their most recent common ancestor, and all descendants of that ancestor.
- Grade** A paraphyletic group, that is, a group that contains an ancestor and some, but not all, of its descendants.
- Laurasia** A supercontinent that contained North America and much of Europe and Asia formed by the breakup of Pangea, and which lasted until the early Cenozoic (late Paleocene, ~56 Ma).
- Osteoderm** An ossified bony plate under the skin.
- Pangea** A global supercontinent that formed during the late Paleozoic era (~335 Ma) and broke apart during the early Mesozoic era (~175 Ma).
- Skull kinesis** The capacity for substantial movement of the skull bones relative to one another, in addition to movement between the upper and lower jaws.
- Synapomorphy** A derived feature shared by an ancestor and its descendants.
- Total clade** A crown clade plus all groups more closely related to the crown clade than to any other clade (i.e. 'stem groups').

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Further Reading