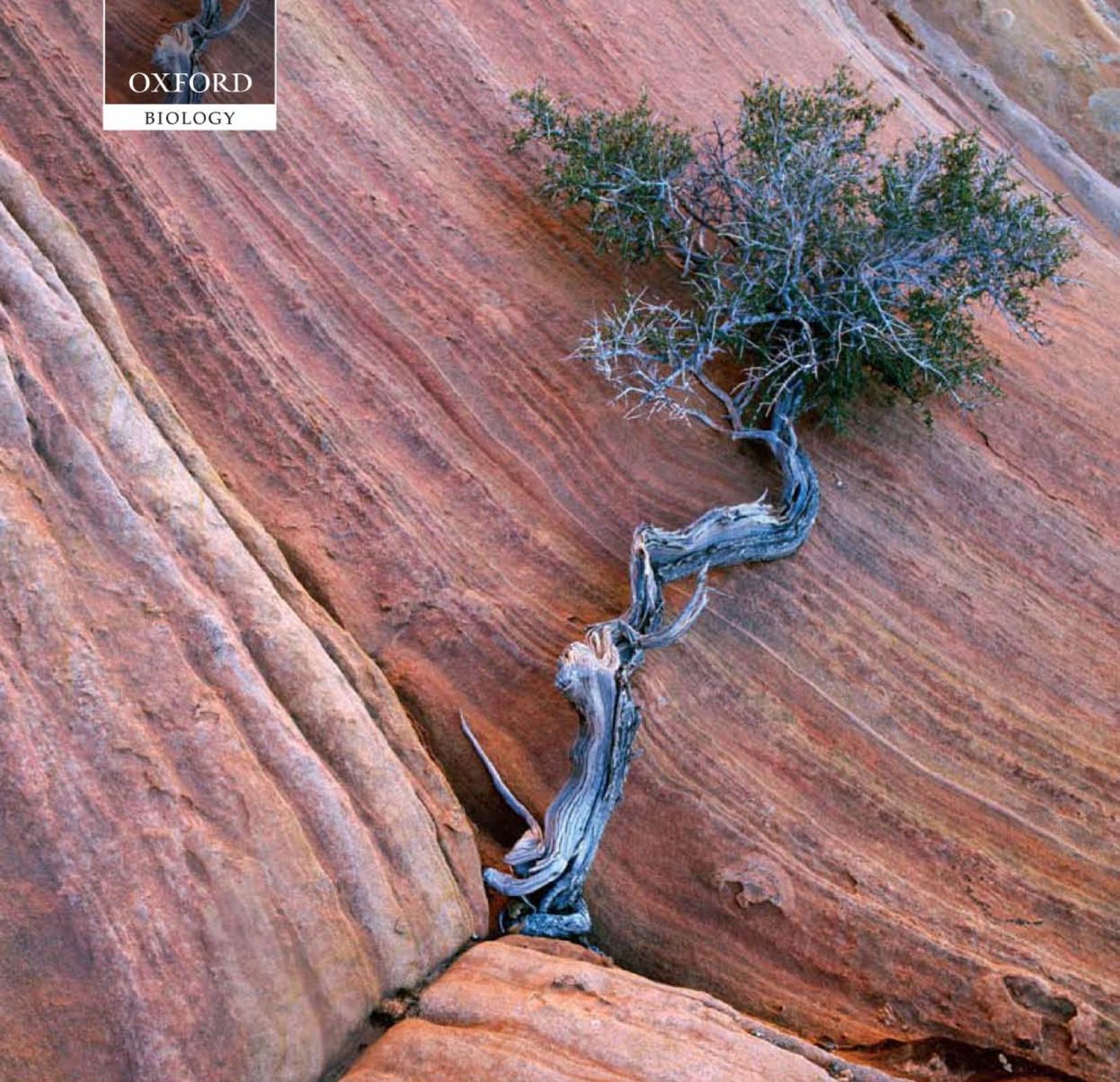


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Lizards, snakes, and amphisbaenians (Squamata)

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Abstract

Living species of lizards, snakes, and amphisbaenians (~8200 sp.) are grouped into 58 families within the sauropsid Order Squamata. Recent phylogenetic analyses of nuclear genes have resulted in major changes in their classification. Iguanian lizards, once considered basal in the squamate tree, are now placed in a highly nested position together with snakes and anguimorph lizards. The squamate timetree shows that most major groups diversified in the Jurassic and Cretaceous, 200–66 million years ago (Ma), possibly related to the breakup of supercontinents. In contrast, five of the six families of amphisbaenians are younger, having arisen during the Cenozoic (66–0 Ma).

The lizards, snakes, and amphisbaenians form a monophyletic group of scaly reptiles, the Order Squamata. They are typically grouped together with the tuataras (Order Rhynchocephalia) in the Subclass Lepidosauria. Male squamates have a pair of unique copulatory organs, hemipenes, located in the tail base. Limb reduction or loss has occurred independently in multiple lineages. Nearly 8200 living species of squamates have been described and placed in ~58 families: ~4900 species in 26 families of lizards (Fig. 1), ~200 species in six families of amphisbaenians, and ~3070 species in 26 families of snakes (1, 2). Here, we review the relationships and divergence times of the families of squamates, excluding snakes (Serpentes), which are treated elsewhere (3).

The classification of squamates was pioneered by Camp (4) and has, until recently, followed the arrangement proposed by Estes *et al.* (5). In it, species were placed in two major groups: Iguania (iguanids, agamids,

and chamaeleonids) and Scleroglossa (all other families). This division was based on multiple morphological characters (5) but emphasized tongue morphology and mode of feeding. Iguanians have muscular tongues and use tongue prehension, a feeding mode which is thought to be primitive, whereas scleroglossans have hard tongues and use jaw prehension. Recently, morphological analyses have continued to find support for this conventional classification of squamates (6).

Historically, three groups of squamates having limb reduction or loss (snakes, amphisbaenians, and dibamids) have been the most difficult to classify, probably because of their specialization and loss of characters. Nonetheless, all three groups have been placed with scleroglossans in most classifications (7, 8). The long, deeply forked tongue and other characters of snakes have allied them with anguimorph lizards, especially the monitor lizards (Varanidae and Lanthanotidae).

The Mesozoic (251–66 Ma) fossil record of squamates is sparse (9). There are no known fossils before the Triassic/Jurassic boundary (200 Ma), although indirect evidence



Fig. 1 Representative squamate reptiles. (A) An iguanid lizard, *Anolis baracoae*, from Cuba (upper left); (B) a sphaerodactylid lizard (*Sphaerodactylus richardsoni*) from Jamaica (upper right); (C) an amphisbaenid amphisbaenian (*Amphisbaena bakeri*) from Puerto Rico (lower left), and a colubrid snake (*Lampropeltis triangulum*), from the United States (lower right). Credits: S. B. Hedges.

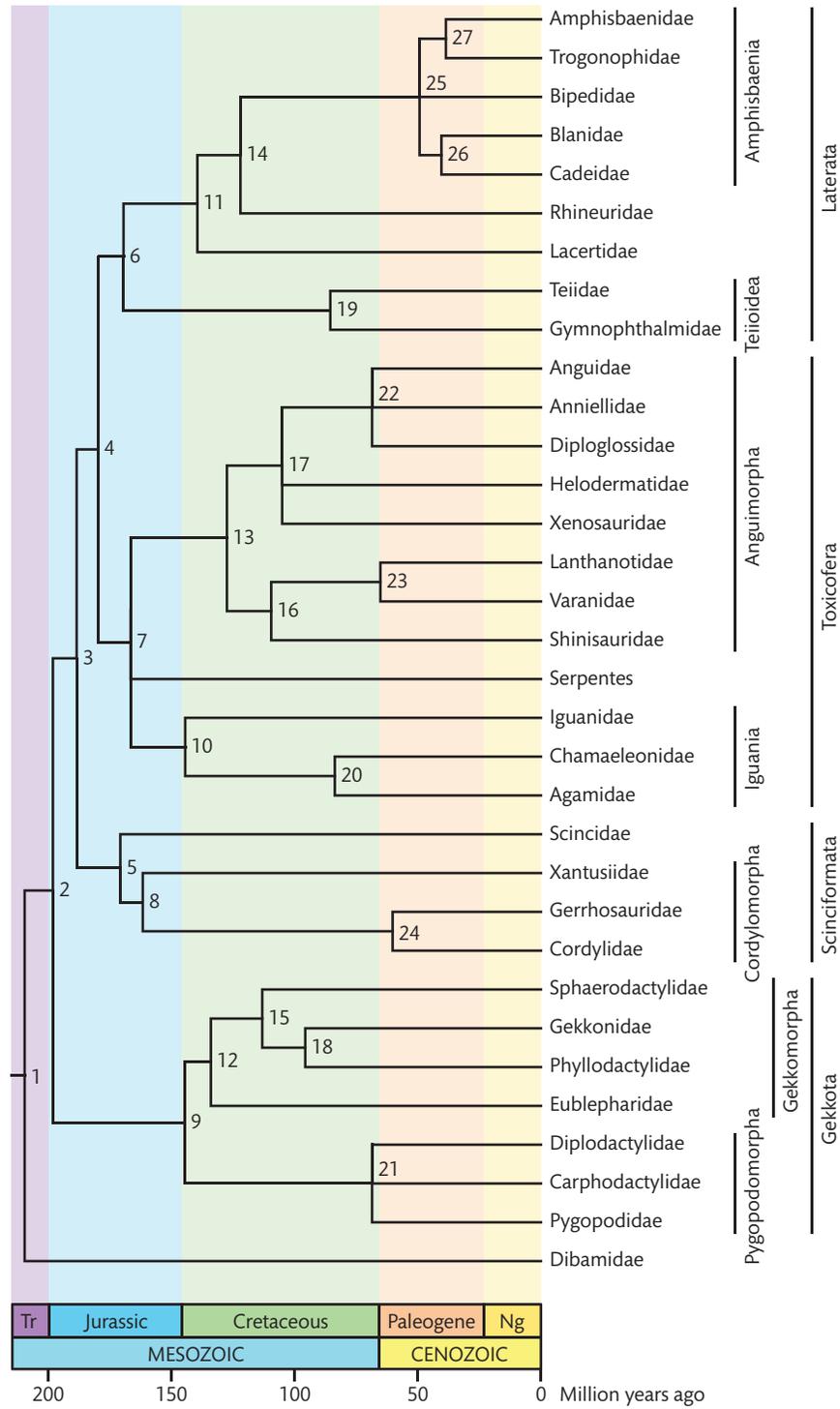


Fig. 2 A timetree of squamate reptiles (Squamata). Divergence times are shown in Table 1. *Abbreviations:* Ng (Neogene) and Tr (Triassic).

Table 1. Divergence times (Ma) and their credibility/confidence intervals (CI) among squamate reptiles (Squamata).

Node	Timetree		Estimates											
	Time	Ref. (22)		Ref. (27)		Ref. (29)		Ref. (25)		Ref. (24)		Ref. (35)	Ref. (38)	
		Time	CI	Time	CI	Time	CI	Time	CI	Time	CI	Time	Time	CI
1	209.4	240	251-221	178.7	184-173	-	-	-	-	-	-	-	-	-
2	197.9	225	240-207	178.7	184-173	190.0	204-176	-	-	-	-	-	250-236	278-208
3	188.3	215	230-199	173.9	179-169	176.0	190-162	-	-	-	-	-	-	-
4	179.7	191	206-179	168.3	174-163	-	-	-	-	-	-	-	-	-
5	170.5	192	209-176	157.6	167-149	162.0	175-149	-	-	-	-	-	-	-
6	169.3	177	193-164	161.6	168-156	-	-	-	-	-	-	-	-	-
7	166.4	178	194-167	163.1	169-158	158.0	171-145	-	-	-	-	-	-	-
8	161.4	179	197-161	143.8	156-132	-	-	-	-	-	-	-	-	-
9	144.6	111	133-90	86.5	95-78	94.0	104-84	144.6	206-85	-	-	-	196-163	233-130
10	144.2	-	-	146.4	154-139	142.0	155-129	-	-	-	-	-	-	-
11	139.3	152	169-136	126.6	139-115	-	-	-	-	-	-	-	-	-
12	133.9	-	-	-	-	-	-	133.9	197-77	-	-	-	195-142	228-111
13	127.3	142	157-113	118.0	125-111	122.0	137-107	-	-	-	-	-	-	-
14	121.9	138	157-121	119.1	131-107	-	-	-	-	108.5	154-76	-	-	-
15	113.0	-	-	-	-	-	-	113.0	161-65	-	-	-	-	-
16	109.5	-	-	110.0	-	109.0	123-95	-	-	-	-	-	-	-
17	105.0	114	129-106	102.0	100-98	99.0	111-87	-	-	-	-	-	-	-
18	95.7	-	-	-	-	-	-	95.7	116-75	-	-	-	-	-
19	85.5	-	-	99.0	99-99	72.0	80-64	-	-	-	-	-	-	-
20	83.5	-	-	-	-	80.0	90-70	-	-	-	-	87	-	-
21	68.6	-	-	-	-	54.0	61-47	68.6	97-40	-	-	-	-	-
22	68.5	-	-	68.5	76-61	-	-	-	-	-	-	-	-	-
23	65.0	-	-	65.0	65-65	-	-	-	-	-	-	-	-	-
24	60.3	-	-	60.3	71-50	-	-	-	-	-	-	-	-	-
25	49.3	46	59-35	48.6	57-41	-	-	-	-	53.2	74-38	-	-	-
26	40.3	-	-	-	-	-	-	-	-	40.3	58-27	-	-	-
27	38.6	32	43-23	32.9	39-27	-	-	-	-	51.0	69-37	-	-	-

Note: Node times in the timetree represent the mean of time estimates from different studies. Note that the gekkotan nodes in the timetree use only the time estimates from the comprehensive gecko study (25) to maintain the tree topology.

suggests that earliest divergences had already occurred by that time. Except for fragmentary remains in Africa and India, all of the Jurassic (200–146 Ma) fossils are from localities on northern continents (Laurasia). The paucity of Mesozoic fossils in general, and especially of those from Gondwana, has hindered biogeographic reconstructions and phylogenetic implications from the fossil record (9).

Initial molecular phylogenies based on subsets of the different families, and those studies using mitochondrial DNA, have tended to give conflicting results (10–17). Phylogenies from mitochondrial DNA usually show

considerable rate variation among branches, particularly long-branch lengths in snakes, and they place snakes outside of all lizards and amphisbaenians (14, 16, 17). The first studies using a nuclear gene (*C-mos*) and comprehensive taxonomic coverage resolved the monophyly of most families that were examined but not interfamilial relationships (18, 19).

In early 2004, the first study using multiple nuclear genes (*C-mos* and *RAG-1*) and broad taxonomic coverage (20) found statistical support that snakes are not the closest relatives of varanid lizards, as was generally

believed. Other groupings in the tree, although weakly supported, suggested that most of the classical phylogeny of squamates, based on morphology, was incorrect. For example, iguanians appeared in a highly nested position in the tree, together with anguimorph lizards and snakes. Also, amphisbaenians clustered with lacertid lizards, xantusiids clustered with scincids and cordylids, and dibamids appeared as the most basal living branch of the squamate tree. All of this implied major reversals and convergences in the key morphological characters used in squamate classification over the last century (4, 5).

Later that year, a second study (21) provided additional support for this new phylogeny of squamates with longer sequences of *RAG-1* and greater taxonomic coverage within lizard families. Some of the weakly supported nodes in the previous study now were significant with non-Bayesian methods, although the interrelationships of snakes, anguimorphs, iguanians, and lacertiforms could not be resolved. A new mitochondrial DNA data set of the *ND2* gene for the same taxa showed some conflicting results, such as the unorthodox nesting of snakes within Iguania, probably a result of long-branch attraction (21).

Subsequently, a study using nine nuclear genes provided further resolution of squamate phylogeny (22). The same groupings defined in the 2004 studies were bolstered, and additional groupings were discovered. A clade of three major squamate groups (iguanians, anguimorphs, and snakes) was defined, and further supported by the discovery of the ability for venom production in all three groups involving a suite of molecular and morphological characters (23). The limbless dibamids were found to be the most basal branch of living squamates, now with significant support. Because this new phylogeny was so different from the classical phylogeny (5), the previous classification based on tongue characters and feeding was abandoned and a new one erected. More recently, new families of amphisbaenians (24) and lizards (25) have been recognized based on molecular phylogenetic analyses, and families once separated from Iguanidae based on morphology are now either not recognized or considered as subfamilies of Iguanidae (26).

New morphological characters were identified that were consistent with the molecular phylogeny and used in the new classification (22). Because all squamate families except Dibamidae have a bifurcated tongue, this large clade was named Bifurcata. The presence of one egg tooth (as opposed to two) defines the next most inclusive clade, Unidentata, which excludes dibamids and gekkotans. Scinciformata includes Scincidae, Xantusiidae, Gerrhosauridae, and Cordylidae. Teiformata includes

the Superfamily Teiioidea (Teiidae and Gymnophthalmidae). The venom clade (23) was named Toxicofera and the lacertid–amphisbaenian group was named Lacertibaenia. Lacertibaenians and teiformatans were grouped into Laterata, most of which have tile-like ventral scales. Toxicoferans and lateratans were grouped into Episquamata (“top squamates”). Several groups of families (Amphisbaenia, Iguania, Anguimorpha, Teiioidea, and Gekkota) agree with previous classifications. Within Iguania, the conventional grouping of chamaeleonids and agamids (Acrodonta) is supported (21).

However, molecular phylogenetic studies in recent years have resolved more of squamate phylogeny than these large clades. Detailed relationships of families are now well supported (20–22, 24, 25, 27), leading to some recent adjustments in the taxonomy (28). For example, the monophyly of the previously defined Varanoidea (Varanidae, Lanthanotidae, and Helodermatidae) has not been supported by molecular evidence (20–22, 27, 29). Also, the monophyly of the Anguidae has been difficult to obtain because the anguid Subfamily Diploglossinae has a similar level of molecular divergence as the Family Anniellidae (21, 27, 30). Thus, the Anguidae was restricted to the Subfamilies Anguinae and Gerrhonotinae, and Diploglossidae was recognized as a family (28) as has been done in the past (e.g., 31).

Two clades of anguimorph families are now defined in molecular analyses that correspond to geography (20–22, 27, 29). The first is a mostly New World (ancestrally North American) clade composed of Anguidae, Anniellidae, Diploglossidae, Helodermatidae, and Xenosauridae. The second is an Old World (ancestrally Asian) clade composed of Lanthanotidae, Shinisauridae, and Varanidae. These clades are so different from previous morphological groupings (e.g., *Shinisaurus* was usually placed in the Xenosauridae and helodermatids were usually associated with varanids and lanthanotids) that they were given new names: Neoanguimorpha for the New World clade and Paleanguimorpha for the Old World clade (28). Within the Neoanguimorpha, the superfamily Anguioidea was restricted to the three closely related families Anguidae, Anniellidae, and Diploglossidae, with the remaining families placed in their own superfamilies, Helodermatoidea (Helodermatidae) and one newly named, Xenosauroida (Xenosauridae). Within the Paleanguimorpha, the Superfamily Varanoidea was restricted to the two closely related families Lanthanotidae and Varanidae, and Shinisauridae was placed in its own superfamily, Shinisauroida (28).

Within geckos (Gekkota), two recent molecular phylogenetic studies (25, 32) have recognized seven families

and defined several well-supported clades, now recognized taxonomically (28): Eublepharoidea (Eublepharidae), Gekkonoidea (Gekkonidae, Phyllodactylidae, and Sphaerodactylidae), and Pygopodoidea (Carphodactylidae, Diplodactylidae, and Pygopodidae). The first two superfamilies were placed in the now redefined Gekkomorpha and the third in the taxon Pygopodomorpha (28). Amphisbaenian relationships are now well supported (24), and likewise their taxonomy has been adjusted (28), with recognition of the Superfamilies Amphisbaenoidea (Amphisbaenidae and Trogonophidae), Rhineuroidea (Rhineuridae), Bipedoidea (Bipedidae), and Blanoidea (Blanidae and Cadeidae). Rhineuroidea was placed in Rhineuriformata and the other three superfamilies in Amphisbaeniformata. The scinciformatan Families Cordylidae and Gerrhosauridae have always been found to be close relatives and were placed in the Superfamily Cordyloidea, and together with Xantusioidea (Xantusiidae) in the taxon Cordylomorpha. Scincomorpha was redefined to include only the Scincoidea with its single family, Scincidae. Finally, within Iguania, the Agamidae and Chamaeleonidae were placed in the Chamaeleonoidea, which in turn was placed in Acrodonta. Iguanidae was placed in Iguanoidea, which in turn was placed in the taxon Neoiguania (28).

Few studies have estimated divergence times among squamate families. In a globin gene sequence study using absolute rates of change, the iguanian–varanid split was estimated as 139–86 million years ago (Ma) and the lizard–snake split as 161–92 Ma (33). In mitochondrial DNA studies, the divergence of scincids and iguanians was estimated as 167 Ma (34) and 158 Ma (13), and the split of agamids and chamaeleonids was estimated as 87 Ma (35). However, some of these estimates may have been influenced by known mitochondrial rate differences among squamates (e.g., the fast rate in snakes) and conflict with the squamate fossil record, particularly the earliest anguimorph fossil at 166 Ma (9), in the context of the new phylogeny.

Only three studies have estimated divergence times among the major lineages of squamates in a comprehensive manner. The first study (22) used nine nuclear protein-coding genes and a Bayesian method (Fig. 2). The second study (27) used published nuclear *RAG-1* sequences (21), and a penalized likelihood method (*RAG-1* was one of the nine genes used in the first study). The third study also analyzed published *RAG-1* sequences with a penalized likelihood method and five fixed calibrations (29). Yet another study used sequences from mitochondrial genomes and a Bayesian method of time estimation, although fewer taxa

were included and the time estimates themselves were not published (17). All studies used calibrations from the tetrapod and squamate fossil record. The relationships obtained in these studies were all similar in general, in that they supported the “new” squamate phylogeny and did not support the basal split between Iguania and Scleroglossa (the conventional morphological classification). However, because the mitochondrial study showed evidence of substantial rate variation among branches (especially snakes), the focus here is on the three studies using nuclear genes and broader taxonomic sampling.

The time estimates in the *RAG-1* studies tended to be younger than those in the nine-gene study of Vidal and Hedges (Table 1). For example, the basal squamate divergences (nodes 1–2) in the *RAG-1* studies were estimated to be 190–178 Ma, considerably later than the nine (nuclear) gene estimate of 240–225 Ma and the mid-Triassic paleontological estimate (9). Hugall *et al.* (29) attributed the difference to the use of two calibration points out of five used by Vidal and Hedges (22) that they considered problematic (difficult to diagnose taxonomically because of limited material): the earliest anguimorph, *Parviraptor* (~166 Ma), and the earliest teiid, *Ptilotodon* (~112 Ma). More recently, Brandley *et al.* (36) went further and claimed that Vidal and Hedges (22) used incorrect calibrations, causing the difference in time estimates, citing Hugall *et al.* (29). However, Brandley *et al.* misinterpreted Hugall *et al.*, because the difference is a matter of opinion, not of correctness. Other paleontologists considered those two fossils to be correctly assigned (9, 37). Nonetheless, these two particular fossils, whether they are correctly assigned or not, are unlikely to explain the difference in molecular time estimates. Wiens *et al.* (27) and Hugall *et al.* (29) both estimated the *Ptilotodon*-constrained node as Jurassic (200–146 Ma), much older than the Cretaceous fossil (112 Ma), and they estimated the *Parviraptor*-constrained node as 162–160 Ma, almost identical in age to that fossil (166 Ma). Moreover, there are other, uncontested, Middle and Late Jurassic fossils of anguimorphs (9) that would similarly constrain that node if *Parviraptor* were not used. The difference in molecular time estimates among those studies may be from the use of smaller data sets and different methods (penalized likelihood rate smoothing) used by Wiens *et al.* (27) and Hugall *et al.* (29) compared with the larger data set (more genes and sites) and Bayesian method used by Vidal and Hedges (22), or from differences in other calibration points.

In addition to those comprehensive studies, three additional timing studies have appeared recently that have

focused on smaller clades of squamate families. One study analyzed divergence times among the six families of amphisbaenians using two mitochondrial genes and Bayesian methods (24). They found that five of the six (all except Rhineuridae) were considerably young, having arisen only in the Cenozoic. The other study used five nuclear genes and nonparametric rate smoothing in a diverse sample of geckos, finding deep (Mesozoic) divergences among most of the six families (25). Another gecko study focused mainly on eublepharids but also presented some time estimates among families of squamates, using mitochondrial DNA sequences and a Bayesian method of time estimation (38). They generally found a great range in divergence times for nodes, with most times being older than those estimated in the other studies.

The timetree of squamates (Fig. 2) represents a synthesis of these various molecular studies, although emphasizing the three comprehensive studies using nuclear genes. It shows that most of the major splits in the tree occurred during the Jurassic and Cretaceous, 200–66 million years ago. The earliest of those divergences took place when all of the continents were joined in a single supercontinent, Pangaea. These included the divergence of dibamids and bifurcatans, gekkotans and unidentatans, and scinciformatans and episquamatanans. Therefore a strong geographic influence in the ancestral distributions of these groups is not expected. As noted, the fossil record is essentially silent on the early biogeographic history of squamates (9).

Pangaea broke into Laurasia and Gondwana in the Jurassic, ~170–150 Ma (39, 40). Considering the timetree and confidence intervals (Table 1), a large number of squamate lineages may have split at this time, including the earliest divergences among scinciformatans (scincids, cordyloids, and xantusiids), toxicoferans (snakes, anguimorphs, and iguanians), lateratans (teiidoids, lacertids, and amphisbaenians), iguanians (iguanooids and chamaeleonoids), and gekkotans (gekkomorphs and pygopodomorphs). The timetree shows early Cretaceous (146–100 Ma) divergences among several gecko families based on the study of Gamble *et al.* (25). Concerning the earliest split, between gekkomorphs and pygopodomorphs (146 Ma), two other nuclear gene studies (22, 29) found much younger dates (111–94 Ma) while a recent mitochondrial gene study (38) found older dates (196–163). Thus there remains considerable uncertainty in the timescale of the gekkotan portion of the timetree. The two major clades of anguimorphs, Neoanguimorpha and Paleoanguimorpha, also diverged in the early Cretaceous (Fig. 2), probably related to the continuing separation of

the continents and rising sea levels, creating (in some cases) inland seas. Divergences among anguiooid and varanoid families apparently occurred near the Mesozoic–Cenozoic boundary (66 Ma).

The late Cretaceous divergence (86 Ma) between Teiidae and Gymnophthalmidae, two primarily South American families, probably occurred in South America where both groups are distributed, although it is not clear how they came to inhabit that continent. Also, if they were widely distributed on the Africa–South America supercontinent at 105 Ma, it is not clear what became of the teioids that presumably inhabited Africa after it split from South America (no fossils or living representatives have been discovered in Africa). The divergence of Chamaeleonidae and Agamidae (84 Ma) postdates the breakup of Gondwana and supports oceanic dispersal as a mechanism to explain the origin of chameleons on Madagascar (41). Likewise, continental breakup is unlikely to explain any of the remaining divergences among lizard families, all in the Cenozoic (Fig. 2). According to squamate timetree, one-third (10) of all families of lizards and amphisbaenians diverged within a few million years of the Mesozoic/Cenozoic boundary, including all three pygopodomorph families, the cordyloids, the varanoids, and the anguiooids. This suggests a possible relationship with the asteroid impact at 66 Ma and the resulting extinctions and ecological changes, although this was also a time of major global sea level change and increasing connections among continents (39, 40, 42). In the case of the amphisbaenians, at least one transatlantic dispersal event in the Cenozoic explains the origin of New World amphisbaenids, representing one-half of all known species of amphisbaenians (24).

Despite the coincidence of early splitting events with the breakup of continents in the Mesozoic, there is yet no clear distributional and fossil evidence to support vicariance as a major mechanism in the early evolution of squamates. Nonetheless, the Laurasian distribution of anguimorphs and the possibly Gondwanan distribution of snakes and iguanians, in the Mesozoic, is intriguing and may reflect early vicariant events (22). More Mesozoic fossil material from the southern continents is needed, along with a better resolved tree of toxicoferans.

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