

Mass extinction of lizards and snakes at the Cretaceous–Paleogene boundary

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The Cretaceous–Paleogene (K-Pg) boundary is marked by a major mass extinction, yet this event is thought to have had little effect on the diversity of lizards and snakes (Squamata). A revision of fossil squamates from the Maastrichtian and Paleocene of North America shows that lizards and snakes suffered a devastating mass extinction coinciding with the Chicxulub asteroid impact. Species-level extinction was 83%, and the K-Pg event resulted in the elimination of many lizard groups and a dramatic decrease in morphological disparity. Survival was associated with small body size and perhaps large geographic range. The recovery was prolonged; diversity did not approach Cretaceous levels until 10 My after the extinction, and resulted in a dramatic change in faunal composition. The squamate fossil record shows that the end-Cretaceous mass extinction was far more severe than previously believed, and underscores the role played by mass extinctions in driving diversification.

evolution | adaptive radiation

Today, lizards and snakes (Squamata) are represented by more than 9,000 living species, which exploit an extraordinary range of ecological niches and habitats; they include insectivores, carnivores, herbivores, and omnivores, as well as terrestrial, arboreal, fossorial, and aquatic forms (1, 2). The history of this radiation extends deep into the Mesozoic. After the appearance of crown squamates in the Jurassic (3), lizards and snakes underwent a Cretaceous radiation (4, 5), and by the late Cretaceous most major groups had appeared, including iguanians, geckos, skinks, anguids, and platynotans (3, 4), as well as many snake lineages (5). However, with the exception of the marine mosasaurs, all major squamate lineages are thought to have survived the end of the Cretaceous. Consequently, the Cretaceous–Paleogene (K-Pg) extinction that ended the Mesozoic is considered to have had little effect on squamate evolution (4, 6, 7).

The K-Pg extinction represents one of the most severe mass extinctions in the history of life (8). Its causes remain a matter of debate (7, 9–12), but suggest that the extinction resulted from the Chicxulub asteroid impact (9–12), when debris shot into the atmosphere by the impact would have darkened the skies, causing a shutdown of photosynthesis and subsequent collapse of the food chain (10–13). Terrestrial ecosystems were particularly hard hit. Notably, the nonavian dinosaurs became extinct at this time (9), but the K-Pg event also resulted in severe extinctions among mammals (14), birds (15), insects (16), and plants (17). Given this, it would be remarkable had squamates not been affected.

In this light, we restudied the squamate fossil record across the K-Pg boundary, focusing on North America. Globally, few fossils are available to address this problem, because (i) squamates are generally small and lightly built, limiting their preservation potential, and (ii) few terrestrial sequences span the K-Pg boundary (17). Western North America is unique, however, in having a rich record of lizards and snakes from both the late Maastrichtian (5, 18–22) and the early Paleocene (23–27), making this the only place in the world where the problem can be studied. Critically, a chronostratigraphic framework (SI Appendix) makes it possible not only to examine patterns of turnover, but also to constrain the timing of extinction.

The only previous study of this problem focused on the Maastrichtian–Paleocene transition in eastern Montana. High turnover was observed for fossil vertebrates across the K-Pg boundary; among squamates, 3 of 11 Maastrichtian species (27%) persisted into the Paleocene (14, 28). However, the limited focus of that study makes it difficult to discern whether this high turnover was a regional or local event; furthermore, the rarity of Paleocene vertebrate fossils raises the possibility that survivors have been overlooked, and that turnover is exaggerated by sampling artifacts (14). Consequently, the concept of a mass extinction of squamates has received little attention.

Here we combine data from the literature (19–27) and museum collections to create a detailed picture of squamate diversity and disparity in the Maastrichtian and Paleocene of North America. This study includes localities from New Mexico to Alberta (Dataset S1) and includes all known species, as well as previously unrecognized Maastrichtian species (SI Appendix).

Systematic Paleontology

A total of 27 lizards and three snakes occur in the late Maastrichtian of North America, including 21 previously recognized forms (19–22) and nine heretofore unreported species (Fig. 1). Thus, this assemblage ranks as one of the most diverse fossil squamate assemblages yet discovered. These species represent a wide range of squamate lineages, many of which are now extinct (Fig. 2).

The fauna is dominated by the extinct Polyglyphanodontia. Previously allied with the Teiidae (20–22), these lizards are now recognized as a distinct clade (3, 29) that may lie outside of Scleroglossa entirely (3). Polyglyphanodontians are characterized by a V-shaped dentary symphysis, a long splenial that slots into the subdental shelf, subapical tooth implantation, and tricuspid teeth. Twelve species are present (Fig. 2). The seven previously recognized species are the polyglyphanodontid *Polyglyphanodon sternbergi* (30) and the chamopsiids *Chamops segnis* (18), *Lepto-chamops denticulatus* (19), *Meniscognathus altmani* (20), *Haptosphenus placodon* (20), *Stypodontosaurus melletes* (21), and *Peneteius aquilonius* (22). Here two previously identified species are placed in Polyglyphanodontia. One, previously referred to Iguanidae (21), is here identified as the polyglyphanodontian *Tripennaculus* n. sp. (SI Appendix). A second, unnamed lizard from the Frenchman Formation of Saskatchewan (21) is placed in Chamopsiidae. In addition, three previously unreported species are recognized here. The first of these species is a chamopsiid, *Socognathus brachyodon* (Fig. 1A), referred to *Socognathus* (21) on the basis of the low yet robust mandible, massive symphysis, and reduced accessory cusps. It differs from *Socognathus unicuspis* in having closely packed, bulbous teeth (SI Appendix). The second is *Obamadon gracilis* (Fig. 1B), a small polyglyphanodontian distinguished by tall,

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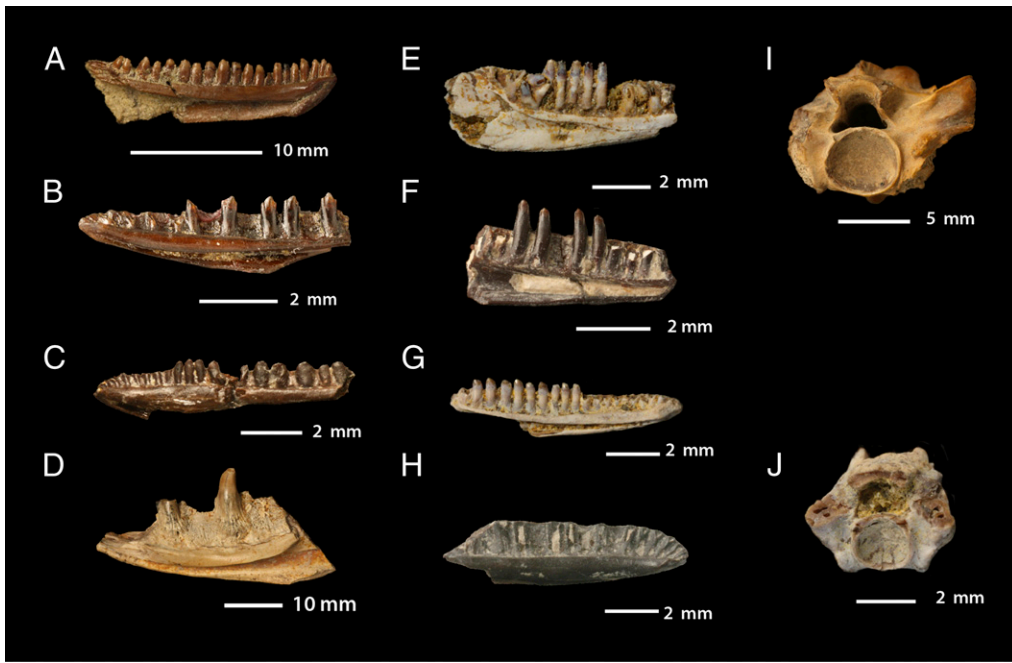


Fig. 1. Maastrichtian lizards and snakes. (A–H) Lizard dentaries; (I and J) snake vertebrae. (A) *Socognathus brachyodon*, n. sp., YPM-PU 16724 Lance Formation, western WY. (B) *Obamadon gracilis*, n. gen et sp., UCMP 128873, Hell Creek Formation, MT. (C) Laramie polyglyphanodont, UCM 42164, Laramie Formation, CO. (D) *Cemeteryus monstruosus* n. gen. et sp., USNM 25870, Hell Creek Formation, MT. (E) *Pariguana lancensis* n. gen et sp., AMNH 22208; Lance Formation, eastern WY. (F) *Lamiasaurus ferox* n. gen et sp., UW 25116A, Lance Formation, southern WY. (G) *Lonchisaurus trichurus* n. gen et sp., AMNH 15446, Lance Formation, eastern WY. (H) Sweetwater lizard, UW 25116B, Lance Formation, southern WY. (I) *Cerberophis robustus* n. gen et sp., UCMP 130696, Hell Creek Formation, MT. (J) Lance alethinophidian, Lance Formation, WY.

slender teeth with large central cusps separated from small accessory cusps by lingual grooves (*SI Appendix*). The third species is an unnamed chamopsiid from Colorado (Fig. 1C), characterized by enlarged back teeth (*SI Appendix*).

Three scincomorphs are present. *Contogenys sloani* (31) has previously been identified as a stem xantusiid (32) but here is placed in the Globauridae, a group of Cretaceous stem scincids (3). *Estescincosaurus cooki* (20) represents a scincoid, but its position within the clade cannot be resolved. *Lonchisaurus trichurus* (Fig. 1G) is a previously unrecognized species distinguished by a long straight dentary, numerous closely packed teeth, and weakly curved crowns with broad, bluntly pointed apices. Its affinities within Scincomorpha remain uncertain.

Anguimorphs rival polyglyphanodontians in diversity (Fig. 2). *Exostinus lancensis* (19) lies on the stem of the extant *Xenosaurus* (20, 33). Anguinae include *Odaxosaurus piger* (19), a basal glyptosaurine, and *Gerhonorotus* spp. (20), a stem gerhonorotine. *Litakis gilmorei* (20), and *Colpodontosaurus cracens* (20) are anguimorphs

of uncertain affinities, neither of which can be placed in any extant clade.

Four varanoid-like platynotans are present: *Palaeosaniwa* sp (20), *Parasaniwa wyomingensis* (19), *Paraderma bogerti* (20), and one heretofore unreported species, *Cemeteryus monstruosus* (Fig. 1D). *Cemeteryus* is a large platynotan distinguished by a massive jaw and short, robust, lingually expanded teeth lacking serrations (*SI Appendix*). *Palaeosaniwa* and *Paraderma* are typically interpreted as crown varanoids (20, 34), but our analysis places these species and *Cemeteryus* on the varanoid stem near *Parasaniwa* (Fig. 2). *Palaeosaniwa* is the largest lizard in the assemblage, and also the largest terrestrial lizard known from the Cretaceous; with an estimated snout-vent length (SVL) of 82 cm, it has a predicted mass of 6 kg (*Dataset S1*).

A single iguanid is present in the assemblage. Until now, there has been no definitive evidence of Iguanidae from the Cretaceous of North America; previous reports of Cretaceous iguanids (21) instead represent polyglyphanodontians. Here we report the oldest iguana known from North America, *Pariguana lancensis*

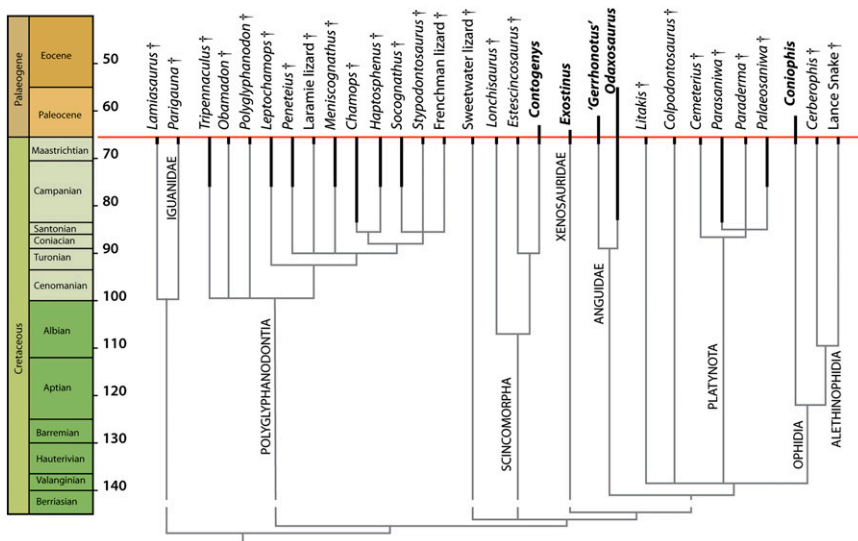


Fig. 2. Systematics of North American squamate assemblage. Adams consensus with alethinophidian placement following a recent study (5). Complete results are provided in *SI Appendix*. Species crossing the K-Pg boundary are shown in bold type.

(Fig. 1E). *Pariguana* shares with iguanians a lip beneath the Meckelian fossa formed by an upfolded ventral margin of the dentary. Posterior extension of the dentary angular process and the anterolateral extension of the coronoid onto the dentary indicate that *Pariguana* is more closely related to crown Iguanidae than are the Asian stem iguanids. *Pariguana* resembles Paleocene iguanids (23) in having teeth with a broad central cusp flanked by minute accessory cusps, but is distinguished by constriction of the Meckelian fossa ahead of the anterior inferior alveolar foramen (*SI Appendix*). The existence of *Pariguana* shows that dispersal of iguanids from Asia to North America occurred in the Cretaceous, not in the Paleocene as previously thought (3).

Two previously unreported lizards of uncertain affinities are also present. *Lamiasaurus ferox* (Fig. 1F) is distinguished by tall, curved crowns with constricted apices and lingual ridges. Present analysis places it as a stem iguanian on the basis of the short splenial. A second, unnamed species (Fig. 1H) comes from southern Wyoming; it represents a nonanguimorph autarchoglossan.

Three snakes are known: the stem snake *Coniophis precedens* (18) and two alethinophidians (5). *Cerberophis robustus* (Fig. 1I) is a large basal alethinophidian (5) previously referred to Boidae (28). *Cerberophis* is distinguished by broad vertebrae with hypertrophied synapophyses, and enlarged prezygapophyses with accessory ridges anteriorly (*SI Appendix*). A vertebral width of 17 mm implies an SVL >1.7 m and a mass >2.9 kg (*Dataset S1*), making *Cerberophis* large enough to potentially prey on any of the Cretaceous mammals, as well as on small dinosaurs and hatchlings of larger dinosaurs. The third species is an unnamed small alethinophidian (5) (Fig. 1J).

Patterns of Extinction

The fauna shows extremely high turnover across the K-Pg boundary. Of the 30 species found in the late Maastrichtian, only five—*Exostinus*, “*Gerrhonotus*,” *Odaxosaurus*, *Contogenys*, and *Coniophis*—occur in the Paleocene. Thus, survival and extinction rates are 17% and 83%, respectively. The survival rate is lower than previously estimated (14), because sample sizes are larger, because taxonomic revision has increased the diversity of the Maastrichtian victims, and because the mistaken report of *Contogenys* from the Hell Creek increased estimates of survival.

It has been argued that high turnover at the K-Pg boundary is in part an artifact caused by poor sampling in the Paleocene (14). To test this hypothesis, we computed species accumulation curves using rarefaction of occurrence data and sample-based (Mao-Tau) (35) rarefaction (Fig. 3). These sampling curves show that the Paleocene is not undersampled relative to the Maastrichtian. Surprisingly, despite the rarity of Paleocene fossils, the fossil record is actually less complete in the Maastrichtian, because (as discussed below) most victims of the extinction have restricted geographic ranges, making them difficult to find. Insofar as sampling artifacts distort the picture, they may make the extinction appear less severe than it actually was.

The extinction resulted in the loss of the most diverse clade of Late Cretaceous lizards, the Polyglyphanodontia, which represents some 40% of Maastrichtian diversity. Many other lineages, including the lineages represented by *Palaeosaniwa*, *Litakis*, *Colpodontosaurus*, *Lamiasaurus*, and *Cerberophis*, disappeared as well. Although we do not use a Linnean taxonomy, these lineages are arguably sufficiently phylogenetically and morphologically distinct to warrant family rank. Thus, the absence of extinction among terrestrial lizard “families” (7) is a taxonomic artifact. In a traditional, Linnean framework (19–21), virtually all families appear to cross the K-Pg boundary (7), because lineages that became extinct were either lumped into modern families or simply excluded from analysis because they could not be classified.

Survival at the K-Pg boundary is highly nonrandom. Small size has been identified as a determinant of survival (36), yet size selectivity is evident even among the squamates. The most striking pattern is the extinction of all large lizards and snakes. The Maastrichtian fauna includes a number of larger forms, including *Palaeosaniwa* and *Cerberophis*, but large squamates are conspicuously absent from the

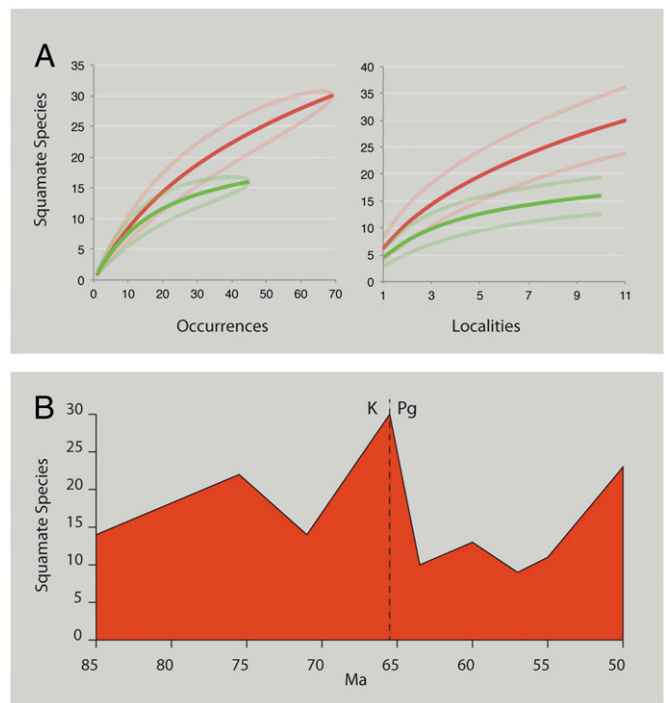


Fig. 3. Comparisons of late Maastrichtian and Paleocene diversity. (A) Late Maastrichtian (Lancian) and early Paleocene (Puercan-Torrejonian). (B) Diversity of lizard genera by land vertebrate age (using range-through assumption), Aquilan to Wasatchian.

Paleocene. The largest known early Paleocene lizard is *Provaranosaurus acutus*. Comparisons with varanids suggest an SVL of 305 mm and a mass of 415 g (*Dataset S1*), compared with an estimated SVL of 850 mm and mass of 6 kg for the largest Maastrichtian lizard, *Palaeosaniwa*. The largest early Paleocene snake is *Helagras prisciformis*, with an estimated SVL >950 mm and a mass >520 g, compared with >1,700 mm and 2.9 kg for the largest Maastrichtian snake, *Cerberophis*.

Because tooth diameter is correlated with SVL (*Dataset S1*), we used tooth diameter to examine the relationship between survival and body size. Average tooth diameter is significantly smaller for the survivors (mean, 0.494 mm) than for victims (mean, 1.07 mm) ($P < 0.05$, t test). We used logistic regression to quantify how survival probability is affected by size. This approach allowed us to use a continuous independent variable (e.g., tooth diameter) to predict a categorical dependent variable (e.g., survival vs. extinction), and to describe that response with a curve. The relationship between survival and tooth diameter is described by the logistic equation $\text{logit}(\text{survival}) = 0.9881 - 4.1350 \times (\text{tooth diameter})$ (model $\chi^2 = 4.384$; $df = 1$; $P = 0.0363$), demonstrating how the odds of survival drop precipitously with increasing size (Fig. 4).

Analysis of selectivity is complicated by the nonindependence of data points, however. For example, the large stem varanoids are related and thus may share features other than body size, such as foraging strategy, breeding biology, or vulnerability to cold. Selection against one of these traits would eliminate these large-bodied forms, creating the appearance of size selectivity. Thus, we used phylogenetically independent contrasts (PIC) analysis to examine the role of phylogeny (*SI Appendix*). Contrasts of survivorship against contrasts for tooth diameter continue to show a negative correlation between survival and size, although the correlation is not significant ($P = 0.37$, two-tailed t test).

The processes behind this size selectivity are not known, but in the absence of photosynthesis, invertebrates feeding on dead plant and animal matter might have been the only available food, favoring the survival of small insectivores (13). In addition, small animals might have been able to seek shelter against the heating

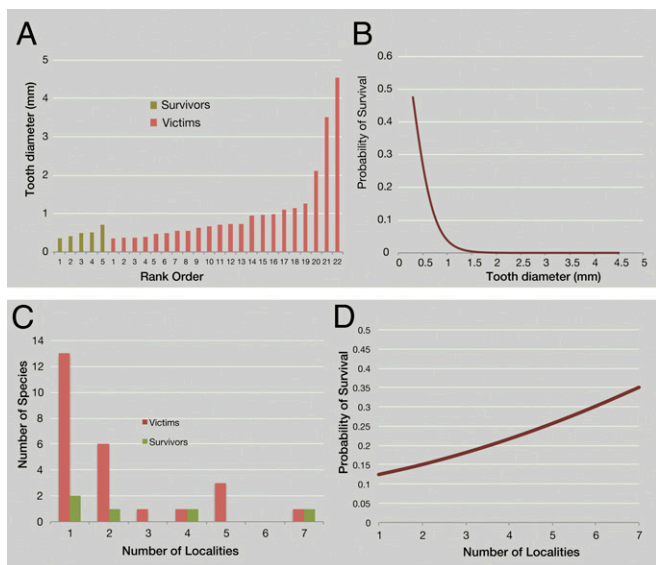


Fig. 4. Selective survivorship of squamates at the K-Pg boundary. (A) Cenograms (size data for species in rank order), with tooth diameter as a proxy for size, for K-Pg survivors and victims. (B) Logistic regression, showing decreasing survival probability at larger sizes. (C) Number of localities occupied by survivors and victims. (D) Logistic regression showing increasing survival probability with increasing geographic range (using number of localities as a proxy for range size).

pulse caused by re-entering ejecta (11) or heavy frosts caused by impact winter (11).

Size selectivity may help explain why nonavian dinosaurs became extinct, suggesting that it was nonavian dinosaurs' failure to evolve a diverse fauna of small-bodied species, rather than a decrease in the diversity of large-bodied forms, that ultimately sealed their fate. A number of small, nonavian dinosaurs are now known from the Late Cretaceous, including alvarezsaurids (37) and microraptorine dromaeosaurids (38), and taphonomic biases almost certainly obscure the true diversity of small dinosaurs (38, 39). However, the fact remains that during the late Maastrichtian, small dinosaurs were vastly outnumbered by other small vertebrates, including a minimum of 30 squamates, 18 birds (15), and 50 mammal species (40). Strikingly, birds—the only dinosaurs to survive—were the only dinosaurs with a high diversity of small-bodied (<5 kg) forms (15). In this context, a discussion of a decline in large dinosaur diversity in the Maastrichtian (9) is perhaps beside the point. A high diversity of large herbivores and carnivores in the latest Maastrichtian would have been unlikely to change the fate of the nonavian dinosaurs, because no animals occupying these niches survived. Instead, the rarity of small dinosaurs—resulting perhaps from being outcompeted by squamates and mammals for these niches—led to their downfall.

Survival also may be influenced by biogeography (41). Survivors occur in more localities (mean, 3 localities) than victims (mean, 2.16 localities), as found for marine invertebrates (41); the difference is not statistically significant, however, by the Mann-Whitney *U* test. The relationship between survival and range is described by the logistic equation $\text{logit}(\text{survival}) = -2.1768 + 0.0228 (\text{occurrences})$ (Fig. 4). Again, the relationship is positive, but not significant. PIC analysis, plotting contrasts of survivorship against range size, shows a weakly positive but not significant association between survival and range size ($P = 0.57$, two-tailed *t* test).

The effects of the K-Pg extinction on squamates also can be shown in terms of morphological disparity. Using tooth diameter as a proxy for body size, it is evident that the early Paleocene fauna has a dramatically reduced range of sizes compared with the Maastrichtian fauna (Fig. 5A). Tooth shape disparity, analyzed using principle component analysis and measured in terms of sum of ranges, product of ranges, sum of variances, or product

of variances (*SI Appendix*), also drops across the K-Pg boundary as forms with specialized ziphodont, brachyodont, and tricuspid teeth disappear (Fig. 5B). The disparity is not significantly lower than expected, however, given the small number of survivors; thus, we cannot reject the hypothesis that the loss of disparity resulted from extinction that is random with respect to tooth shape, rather than from selection against particular morphotypes (*SI Appendix*).

Critically, stratigraphic data make it possible to constrain the tempo of turnover, which is necessary to test competing hypotheses about the causes of the extinction. The vast majority of the species that became extinct can be shown to persist high in stratigraphic section, and many have a last occurrence less than 300,000 y before the Chicxulub impact (*SI Appendix*). Although the precise age of last occurrence cannot be estimated in all cases, we emphasize that the assemblage described here is as close as we can come to providing a picture of the fauna just before the Chicxulub impact. In particular, because many genera persisted for 10 My or longer (Fig. 6), and because vertebrate faunas showed little turnover in the late Maastrichtian (42, 43) it is unlikely that a significant number of these species became extinct in the short intervals separating these localities from the K-Pg boundary.

It has been argued that environmental stresses in the latest Maastrichtian, including climate change and sea level change, contributed to the end-Cretaceous mass extinction by causing a decline in diversity leading up to the K-Pg boundary (9). Discussions of diversity have tended to focus on dinosaurs, but whether they experienced a minor decline during the Maastrichtian (9) or did not (10, 42, 43), the persistence of an exceptionally diverse lizard and snake fauna just before the K-Pg extinction argues against the idea that late Maastrichtian terrestrial ecosystems were stressed before the Chicxulub impact. The available evidence suggests instead that extinctions among the squamates were abrupt and coincided with the K-Pg boundary, supporting the hypothesis that the Chicxulub asteroid impact was the sole cause of the end-Cretaceous mass extinction.

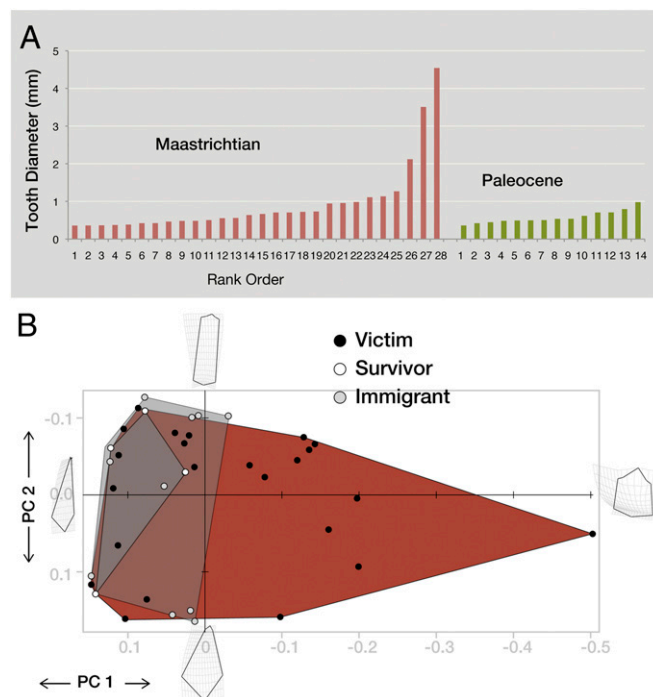


Fig. 5. Disparity of late Maastrichtian and early Paleocene squamates. (A) Cenograms showing Maastrichtian and Paleocene size disparity. (B) Comparison of shape disparity in teeth of Maastrichtian and Paleocene squamates, showing results of a principle components analysis of 2D landmark data. The Maastrichtian fauna is circumscribed by the red hull, with survivors bounded by a dark-gray hull and survivors plus immigrants bounded by a light-gray hull.

Recovery and Radiation

Extinction at the K-Pg boundary was followed by recovery in the Paleocene and Eocene. A number of new lizard lineages occur in the basal Paleocene, notably the stem varanoid *Provaranosaurus*, xantusiids, and amphisbaenians (27). These may represent opportunistic invaders that colonized the area in the aftermath to exploit niches left vacant by the extinction, as seen among mammals (10, 44). Despite this, early Paleocene diversity is considerably lower than late Maastrichtian diversity (Fig. 3). Subsequently, ecological release provided by the extinction allowed the survivors to stage an adaptive radiation, paralleling the adaptive radiations staged by mammals (6, 45, 46), birds (46, 47), and fish (48). The community that emerges in the early Eocene is dominated by groups that are either minor components of the Cretaceous fauna or unknown from the Cretaceous, particularly the Anguinae, Iguanidae, Xantusiidae, Macrostromata, and Amphisbaenia (Fig. 6). However, diversity does not approach Cretaceous levels until the early Eocene, 10 My later, when diversity rapidly increases (Fig. 3B) with the onset of late Paleocene–early Eocene global warming (49). Thus, lizards recovered more slowly than mammals, which rebounded to Maastrichtian diversity levels within 1.5 My of the K-T extinction (44), and exceeded Cretaceous diversity within 5 My of the extinction (45) as they radiated to occupy niches left open by dinosaurs. Unlike mammals, however, squamates appear to have simply reoccupied the niches they occupied before the extinction. This reoccupation of niches was also delayed; by the middle Paleocene, lizards had yet to recover the range of body sizes and morphotypes found in the Maastrichtian (Fig. 5).

The end-Cretaceous extinction of squamates was likely a global phenomenon. As in North America, the Late Cretaceous of Asia is dominated by archaic forms (50, 51), including Polyglyphanodontia and stem members of Iguanidae, Acrodonta, Scincidae, Gekkota, and Varanidae (3), all of which are absent from the Paleogene. Poor stratigraphic constraint makes it impossible to address the timing of these extinctions, but the dramatic turnover of the Asian fauna from the Cretaceous to the Paleogene (51) is consistent with a worldwide extinction of squamates at the end of the Cretaceous. The disappearance of the giant marine Mosasauridae from the world's oceans (4, 6, 7) underscores the reach of this extinction. Our analysis focuses on terrestrial forms, but including mosasaurs would increase estimates of extinction rates and especially of disparity loss. Finally, the appearance of lacertids in the Paleocene of Europe (52), derived acrodonts in the Early Eocene of Asia (53), boid snakes in the Paleocene of South America (54), and caenophidian snakes in the Early Eocene of India (55) document the diversification of these lineages in the aftermath of the K-Pg extinction, suggesting that the Paleogene radiation of squamates was global as well.

Discussion and Conclusions

The squamate fossil record shows that the Chicxulub asteroid impact coincides with severe extinction at the species level, the loss of many branches of the squamate tree, and reduced morphological disparity. Although the fossil record (4) and the molecular clock (56) agree that many squamate clades originated in the Cretaceous, perhaps as part of the “Cretaceous Terrestrial Revolution” (57), these patterns are not inconsistent with mass extinction, given that clades can survive the loss of the majority of their members. The K-Pg extinction ultimately led to the diversification of the lizards and snakes that dominate the fauna today, as the ancestors of modern groups literally emerged from the ashes of the asteroid impact. Thus, the squamate fossil record provides a striking example of how mass extinction works as a form of creative destruction, and shows how the origins of the modern biota can be understood only in light of catastrophes occurring in deep time.

Materials and Methods

To investigate the relationships of the Cretaceous lizards, we conducted a morphological phylogenetic analysis using a new squamate matrix (3) and then added 27 Maastrichtian lizards and *Coniophis*, along with 12 new

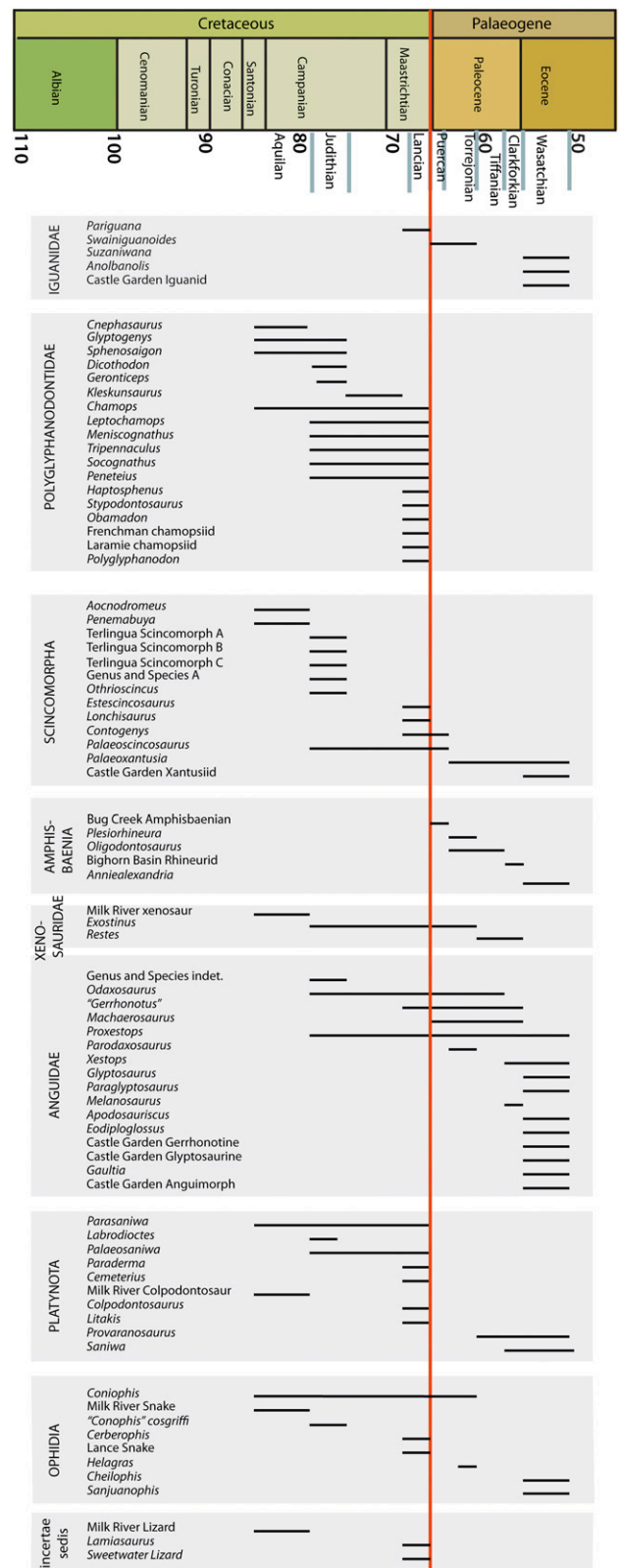


Fig. 6. Cretaceous–Paleogene faunal succession. The Cretaceous fauna is dominated by Polyglyphanodontidae, whereas the Paleogene fauna is dominated by Anguinae and Iguanidae.

characters, for a total of 219 species and 622 characters (Dataset S2). Analyses were conducted using PAUP* 4.0 b10 to implement 10 runs of the parsimony ratchet (200 iterations, 25% reweighting) to find a series of

shortest trees. Heuristic search was then used to generate 100,000 trees to estimate the strict and Adams consensus (*SI Appendix*). Relationships of other snakes follow a recent study (5).

To investigate sampling effects, sample-based rarefaction (*SI Appendix*) with EstimateS was used to compare the quality of the Maastrichtian and Paleocene fossil records. Selectivity with respect to body size and range size were investigated using logistic regression. PIC analysis was conducted using Mesquite. Mass estimates for lizards and snakes were conducted by regressing jaw and vertebral length against SVL, and then using regression equations to estimate mass (*Dataset S1*). Morphological disparity was studied using tooth

diameter to examine size disparity, and landmark analysis was conducted using TPSDig and TPSRelW to examine shape disparity (*SI Appendix*).

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