

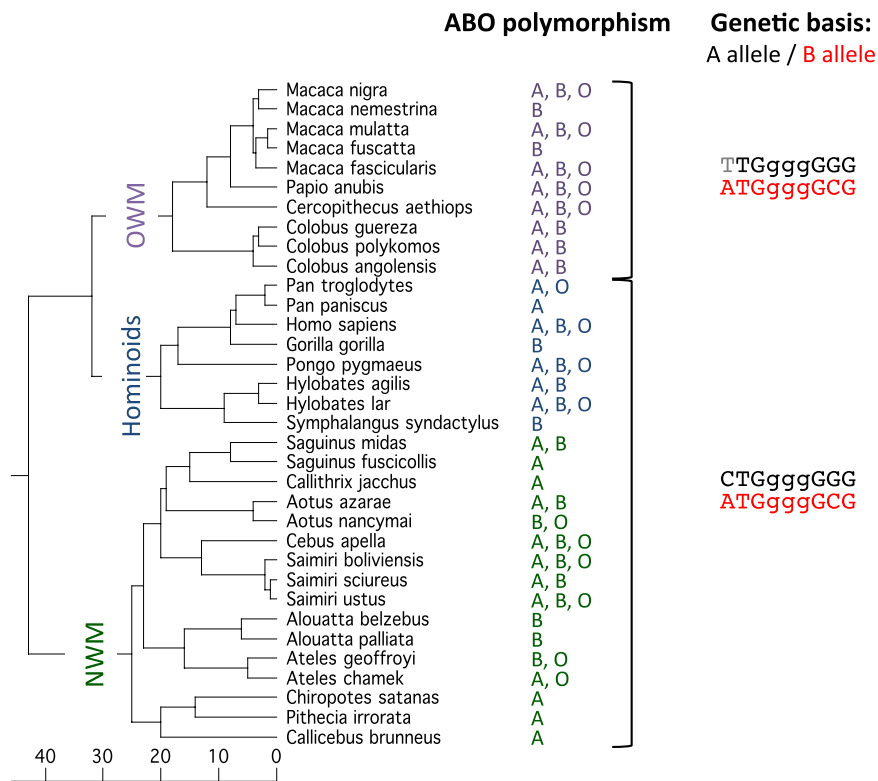
# Corrections

## EVOLUTION

Correction for “The ABO blood group is a trans-species polymorphism in primates,” by Laure Ségurel, Emma E. Thompson, Timothée Flutre, Jessica Lovstad, Aarti Venkat, Susan W. Margulis, Jill Moyse, Steve Ross, Kathryn Gamble, Guy Sella, Carole Ober, and Molly Przeworski, which appeared in issue 45,

November 6, 2012, of *Proc Natl Acad Sci USA* (109:18493–18498; first published October 22, 2012; 10.1073/pnas.1210603109).

The authors note that Fig. 1 appeared incorrectly. Some ABO polymorphism statuses have been corrected. The corrected figure and its legend appear below.



**Fig. 1.** The phylogenetic distribution of ABO phenotypes and genotypes. Shown is a phylogenetic tree of primate species, with a summary of phenotypic/genotypic information given in the first column, and the genetic basis for the A versus B phenotype provided in the second column (functionally important codons at positions 266 and 268 are in uppercase letters). See Dataset S1 for the source of information about phenotypes/genotypes. Only species with available divergence times are represented here (34 of 40). The phylogenetic tree is drawn to scale, with divergence times (on the x axis) in millions of years taken from ref. 29. OWM, Old World monkeys; NWM, New World monkeys. Under a model of convergent evolution, these data suggest that A is the ancestral allele, and a turnover (e.g., a neutral substitution) occurred on the branch leading to Old World monkeys. If instead, B were ancestral, all Old World monkeys would have had to serendipitously converge from ATG to TTG to encode a leucine, whereas all New World monkeys and hominoids would have had to converge to the CTG codon.

[www.pnas.org/cgi/doi/10.1073/pnas.1304029110](http://www.pnas.org/cgi/doi/10.1073/pnas.1304029110)

## EVOLUTION; EARTH, ATMOSPHERIC, AND PLANETARY SCIENCES

Correction for “Mass extinction of lizards and snakes at the Cretaceous–Paleogene boundary,” by Nicholas R. Longrich, Bhart-Anjan S. Bhullar, and Jacques A. Gauthier, which appeared in issue 52, December 26, 2012, of *Proc Natl Acad Sci USA* (109:21396–21401; first published December 10, 2012; 10.1073/pnas.1211526110).

The authors note the following: “The genus name *Lamiasaurus*, which we proposed for a new lizard from the Late Cretaceous of Wyoming, is preoccupied by *Lamiasaurus* Watson 1914 (1), a tapinocephalid therapsid from the Permian of Africa. We therefore propose the name *Lamiasaura* for the Wyoming lizard; its type species is *Lamiasaura ferox*, also proposed in our paper. Furthermore, holotypes were figured for this and other newly proposed species but not explicitly identified in the text. We designate types and provide diagnoses as follows. *Cemeterius monstrosus*, holotype: United States National Museum 25870. Diagnosis: large stem varanoid characterized by a deep, massive jaw, teeth short, unserrated, robust, and labiolingually expanded. *Cerberophis robustus*, holotype: University of California Museum of Paleontology 130696. Diagnosis: medium-sized (~2 m) alethinophidian, trunk vertebrae with broad, flat ventral surface, hypertrophied synapophyses, large, massive prezygapophyses with rudimentary prezygapophyseal processes and anterior ridges; neural arch with dorsolateral ridges, moderately tall neural spine. *Lamiasaura ferox*, holotype: University of Wyoming 25116A, left dentary with four teeth. Diagnosis: dentary straight, tapered in lateral view; teeth widely spaced, crowns weakly recurved, crowns with bottleneck constriction between the base and apex, low mesial and distal cusps, and ridged lingual surface. *Lonchisaurus trichurus*, holotype: American Museum of Natural History 15446. Diagnosis: dentary long, low, and weakly bowed in lateral view; tooth crowns robust, weakly recurved, with weakly pointed crowns; tooth bases wider labially than lingually, tooth replacement reduced, coronoid overlaps dentary laterally. *Obamadon gracilis*, holotype: University of California Museum of Paleontology 128873. Diagnosis: small polyglyphanodontian characterized by the following combination of characters: dentary slender, symphysis weakly developed, tooth implantation subpleurodont, teeth lack basal expansion, tooth crowns with a tall central cusp separated from accessory cusps by deep lingual grooves. *Pariguana lancensis*, holotype: American Museum of Natural History 22208. Diagnosis: small iguanid; teeth tall, slender, with tapering crowns and weak accessory cusps; coronoid extended onto lateral surface of jaw below last tooth, Meckelian groove constricted suddenly ahead of anterior inferior alveolar foramen. *Socognathus brachyodon*, holotype: Yale Peabody Museum (Princeton University Collection) 16724. Diagnosis: *Socognathus* with posterior teeth having strongly swollen, weakly tricuspoid crowns.”

“This correction formally validates the taxa proposed in our 2012 paper; thus, those taxa should be attributed to this note and accordingly dated as March 19, 2013.”

“We thank Christian Kammerer and Christopher Taylor for bringing these two issues to our attention.”

1. Watson DMS (1914) The Deinocephalia, an order of mammal-like reptiles. *Proceedings of the Zoological Society of London* 749–786.

[www.pnas.org/cgi/doi/10.1073/pnas.1303907110](http://www.pnas.org/cgi/doi/10.1073/pnas.1303907110)

## NEUROSCIENCE, PSYCHOLOGICAL AND COGNITIVE SCIENCES

Correction for “Sensory adaptation as optimal resource allocation,” by Sergei Gepshtein, Luis A. Lesmes, and Thomas D. Albright, which appeared in issue 11, March 12, 2013, of *Proc Natl Acad Sci USA* (110:4368–4373; first published February 21, 2013; 10.1073/pnas.1204109110).

The authors note that, due to a printer’s error, some text appeared incorrectly.

On page 4368, right column, third full paragraph, line 6 “in Fig. 2A” should instead appear as “in Fig. 2B”.

On page 4369, right column, second full paragraph, line 7 “in Fig. 2A” should instead appear as “in Fig. 3A”.

On page 4370, left column, fourth full paragraph, lines 1–3 “In Fig. 4A, sensitivity changes are plotted for two speeds (Fig. 4A, Upper) and for the entire domain of the sensitivity function (Fig. 4A, Lower)” should instead appear as “In Fig. 4B, sensitivity changes are plotted for two speeds (Fig. 4B, Upper) and for the entire domain of the sensitivity function (Fig. 4B, Lower)”.

On page 4372, left column, first full paragraph, line 3 “cortical visual area middle temporal (MT)” should instead appear as “middle temporal (MT) cortical visual area”.

On page 4372, right column, second full paragraph, lines 2–3 “as illustrated in Fig. 2A for experiment 1 and Fig. 3A for experiment 2” should instead appear as “as illustrated in Fig. 3A for experiment 1 and Fig. 2A for experiment 2”.

[www.pnas.org/cgi/doi/10.1073/pnas.1304728110](http://www.pnas.org/cgi/doi/10.1073/pnas.1304728110)

## CHEMISTRY

Correction for “Enhanced surface hydrophobicity by coupling of surface polarity and topography,” by Nicolas Giovambattista, Pablo G. Debenedetti and Peter J. Rossky, which appeared in issue 36, September 8, 2009, of *Proc Natl Acad Sci USA* (106:15181–15185; first published August 14, 2009; 10.1073/pnas.0905468106).

The authors note the following: “Recalculations confirm some of the conclusions reported in our paper but do not confirm others. Specifically, we confirm that (i) polar surfaces can be hydrophobic, (ii) capillary evaporation can occur when water is confined between “polar hydrophobic” nanoscale surfaces, and (iii) inversion of surface polarity can alter the surface hydrophobicity (i.e., water contact angle). However, because of the sensitivity of the results to the value of the Ewald wave vector cutoff parameter  $m_{\max}$  for the model surface studied, the reported observation that adding polarity to an apolar silica-based surface can enhance hydrophobicity beyond that of the original apolar surface is not confirmed.

“We thank Zhonghan Hu for bringing to our attention discrepancies between his computer simulation results and some of our calculations reported in the above-cited PNAS paper; Richard C. Remsing and John D. Weeks for generously sharing their results with us; and Sapna Sarupria, Amish Patel, and Sumit Sharma for useful discussions. Additional details regarding the recalculations are available from the authors upon request.”

[www.pnas.org/cgi/doi/10.1073/pnas.1304562110](http://www.pnas.org/cgi/doi/10.1073/pnas.1304562110)

# 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,

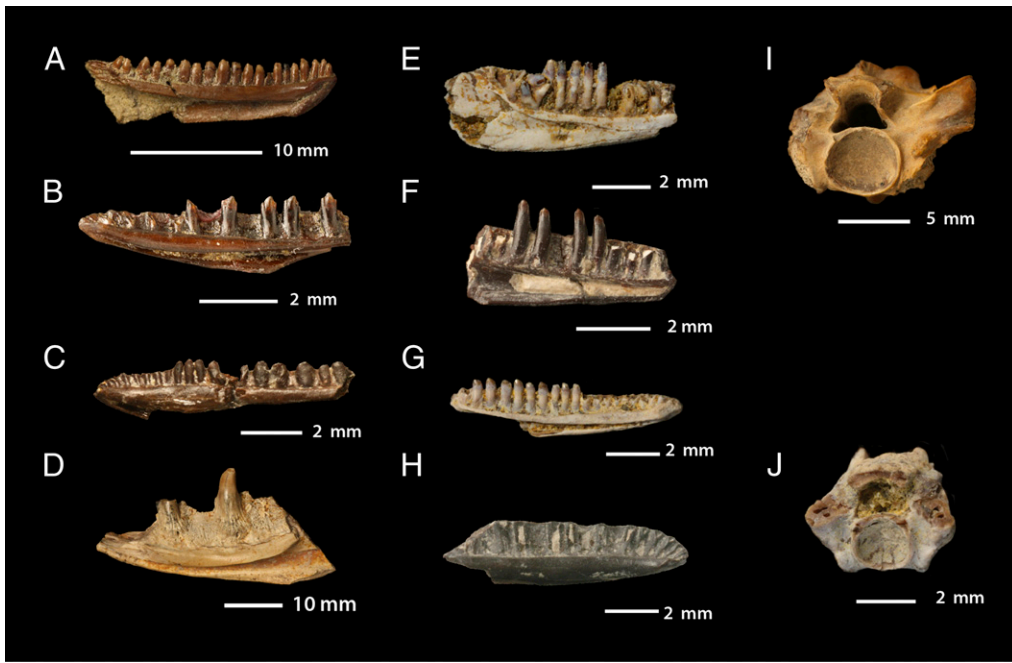
Author contributions: N.R.L. designed research; N.R.L., B.-A.S.B., and J.A.G. performed research; J.A.G. contributed new reagents/analytic tools; N.R.L., B.-A.S.B., and J.A.G. analyzed data; and N.R.L. wrote the paper.

The authors declare no conflict of interest.

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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*).

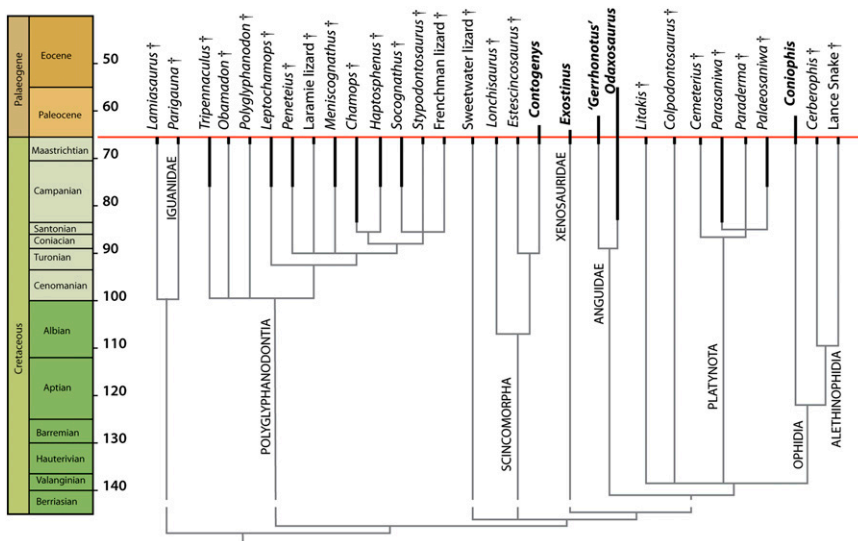
Three scincomorphs are present. *Contogenys sloani* (31) has previously been identified as a stem xantusiid (32) but here is placed in the Globauridae, a group of Cretaceous stem scincids (3). *Estescincosaurus cooki* (20) represents a scincoid, but its position within the clade cannot be resolved. *Lonchisaurus 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).

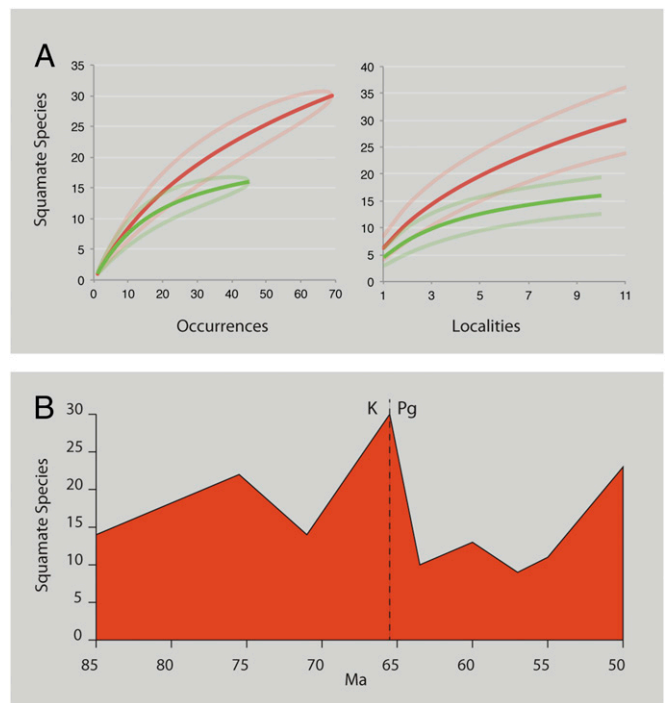
### Patterns of Extinction

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



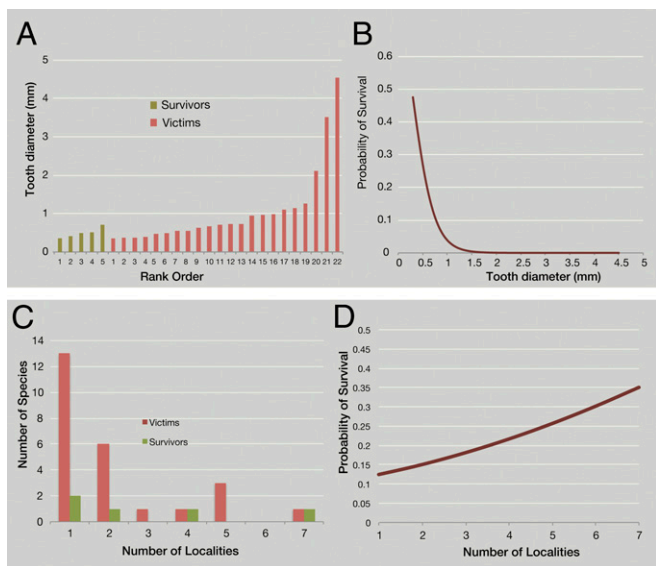
**Fig. 3.** Comparisons of late Maastrichtian and Paleocene diversity. (A) Late Maastrichtian (Lancian) and early Paleocene (Puercan-Torrejonian). (B) Diversity of lizard genera by land vertebrate age (using range-through assumption), Aquilan to Wasatchian.

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.

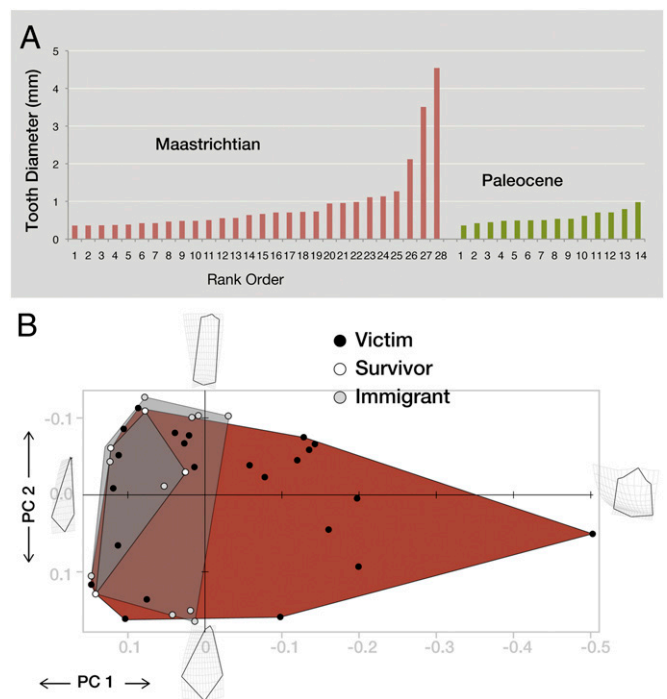
Survival also may be influenced by biogeography (41). Survivors occur in more localities (mean, 3 localities) than victims (mean, 2.16 localities), as found for marine invertebrates (41); the difference is not statistically significant, however, by the Mann-Whitney *U* test. The relationship between 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.



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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