SCIENTIFIC REPORTS
natureresearch

OPEN

Two-step extinction of Late Cretaceous marine vertebrates in northern Gulf of Mexico prolonged biodiversity loss prior to the Chicxulub impact

Takehito Ikejiri[1,2*], YueHan Lu[2] & Bo Zhang[2]

Recent studies on mass extinctions are often based on the global fossil record, but data from selected paleogeographic regions under a relatively constant paleoenvironmental setting can also provide important information. Eighty-nine marine vertebrate species, including cartilaginous and bony fish and marine reptiles, from northern Gulf of Mexico – located about 500 km from the Chicxulub crater – offer a unique opportunity to determine an extinction process during the last 20 million years of the Late Cretaceous. Our diversity data show two separate extinction events: (i) the 'Middle Campanian Crisis' (about 77 Mya) and (ii) the end-Maastrichtian (66 Mya) events. Whether this stepwise pattern of extinctions occurred locally or globally cannot be determined at present due to the lack of a dataset of the marine vertebrate record for reliable comparison. However, this stepwise pattern including the Middle Campanian and end-Maastrichtian events for, at least, a 13 million-year interval indicates long-term global marine environmental changes (e.g., regression, ocean water chemistry change). Because most Cretaceous marine vertebrates already disappeared in the Gulf of Mexico prior to the latest Maastrichtian, the Chicxulub Impact may not be considered as the most devastating extinction event for the community.

The end-Cretaceous mass extinction event has been intriguing many researchers for decades as one of the most fascinating topics in Earth's history[1,2], but the main cause of this devastating incident is still under hot debate. Several competing hypothetical scenarios have been regularly studied, including large bolide impacts (e.g., the Chicxulub), extensive volcanisms (the Decan Trap), global sea-level changes, and so on. This ambiguity often comes from types of data used to quantify and determine extinction patterns, besides a complex nature of the process. Also, types of data, such as global (strictly based on a broad geologic time scale) or local (a selected geographic region in ecologic time), may provide a different view of mass extinctions[3]. The latter type, the bottom-up approach, can be specifically important for filling missing pieces of a puzzle for an overview of a mass extinction event, besides the global data-based top-down approach.

The top-down approach based on global data tends to have been popular for mass extinction studies of Mesozoic marine vertebrate[4–8]; however, data from a specific region is generally scarce in the literature[9–11]. In contrast to marine vertebrates, extinction patterns have been documented well in marine invertebrate and plankton taxa using the bottom-up approach, such as layer- or strata-level occurrence in scoped geographic regions. This tendency of taxonomic preference for mass extinction studies raises the question of whether marine vertebrates exhibit a different extinction pathway when compared to non-vertebrate marine taxa, possibly, due to unique ecological habitats (e.g., tiering, motility, feeding mechanism[3]), paleogeographic distributions, and/or species longevity.

We present overall extinction patterns of Late Cretaceous marine vertebrates (cartilaginous fish, bony fish, and marine reptiles) from northern Gulf of Mexico primarily following a preliminary study[12]. This study focuses on the fossil record from northern Gulf of Mexico (the current location of Alabama in the Southeastern U.S.A)

[1]Alabama Museum of Natural History, University of Alabama, Tuscaloosa, AL, 35487, USA. [2]Department of Geological Sciences, University of Alabama, Tuscaloosa, AL, 35487, USA. *email: ikejiri1859@gmail.com

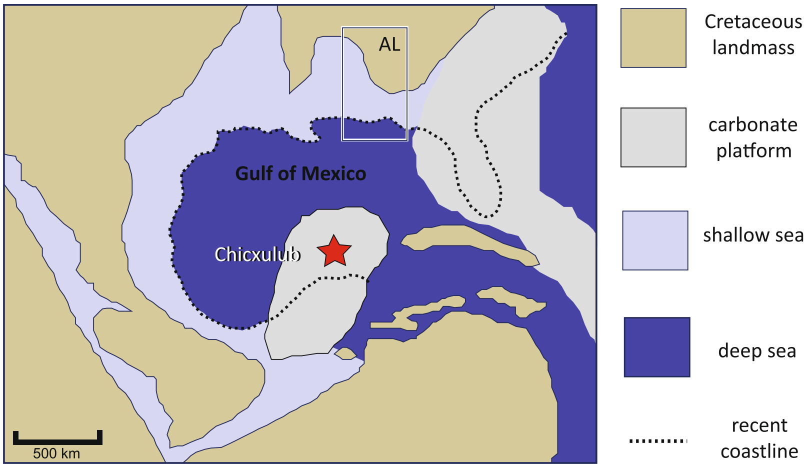


Figure 1. Paleogeographic map of the Gulf of Mexico about 66 million years ago. The red star indicates the position of the Chicxulub impact site. The current position of Alabama (AL) denoted by the white box is approximately 500 km from the impact site. The Mississippian Embayment is located on the left side of the symbol AL. The map was modified from Scotese[82].

Stratigraphic units	Age	Geologic units	Genus & species counts[a]	Specimen (all)[a]	counts (w/ taxonomic ID)
Unit 5	upper Maastrichtian	Prairie Bluff Chalk Fm Providence Sandstone Fm	12 gen., 16 spp. 1 gen., 1 sp.	203 3	96 –
Unit 4	lower Maastrichtian	Ripley Fm	4 gen., 9 spp.	139	37
Unit 3	middle to upper Campanian	Demopolis Chalk Fm	10 gen., 23 spp.	211	63
Unit 3	lower Maastrichtian	Bluffport Marl Mbr*	1 gen., 1 sp.	40	—
Unit 3	moddle to upper Campanian	Cusseta Sand Mbr**	3 gen., 3 spp.	9	—
Unit 3	middle Campanian	Arcola Limestone Mbr***	5 gen., 5 spp.	21	—
Unit 2	lower to middle Campanian	Mooreville Chalk Fm	33 gen., 66 spp.	6,147	1980
Unit 2	lower to middle Campanian	Blufftown Fm		216	—
Unit 1	upper Santonian	Eutaw Fm	12 gen., 49 spp.	943	461

Table 1. List of five stratigraphic units (used as time bins for this study) based on Upper Cretaceous geologic units (formations and members) in Alabama. Species and genus counts and rock volume of each geologic unit (based on surface area and volume) are compared. Key lithological features are listed in Supplementary Table S1. Data for taxonomic counts are available in Supplementary Table S3. [a]Including specimens with uncertain taxonomic identification (data updated from Ikejiri *et al.*[12]). *A part of the Demopolis Chalk Fm. **A part of the Reply Fm. ***A part of the Mooreville Chalk Fm.

(Fig. 1). This narrowly selected geographic region can be important for marine vertebrate extinctions in the following aspects. First, successive geologic units of an over 20 million-year interval of the latest Cretaceous exist in the area (Supplementary Fig. S1). Those strata allow investigating the long-term diversity and extinction processes. Second, the region was paleoenvironmentally consistent to some degree (i.e., offshore marine environment near the Mississippian Embayment along with the southern coast of the Appalachia landmass[13]). Third, Alabama has a long history of scientific investigations and systematic fossil collecting since the early 19th Century[14,15]. This effort leads to a tremendous amount of fossil specimens, which makes it possible to apply the bottom-up approach to understanding extinction patterns. Lastly, Alabama has located about 500 km from the Chicxulub impact site in the Cretaceous Gulf of Mexico. This physical distance is paleogeographically intriguing when determining a magnitude of the asteroid impact on the marine vertebrate fossil record through the K-Pg boundary (Supplementary Fig. S2).

To quantify diversity and extinction patterns of Cretaceous marine vertebrates, species counts, percentages, and three types of rates are compared in five-time bins (stratigraphy-based units) over a 20 million year-interval (Table 1). Species occurrences including and excluding singletons were analyzed separately for comparisons. Data are analyzed on not only all marine vertebrates but also three finer taxonomic groups (cartilaginous and bony fish and marine reptiles) and some selected key Cretaceous taxa (family or order levels) to determine extinction selectivity. Moreover, other major extinction events, besides the end-Maastrichtian event, are investigated in various taxonomic groups. Following those themes based on the local data, we will discuss the possibility of the global phenomenon for marine vertebrates and other marine taxa (invertebrates and plankton) and a possible cause(s) of extinction events.

Raw data						
	County	Locality	Surface area[a]	Thickness maximum[b,c]	Thickness median[b,c]	Duration (median)[d]
	(#)	(#)	(km^2)	(m)	(m)	(m.y.)
Unit 1	12	19	4539	61	46	3
Unit 2	17	79	3978	183	96	5
Unit 3	7	39	3168	151	140	8
Unit 4	8	21	2045	76	43	2
Unit 5	7	28	1884	91	59	4
Kendall's tau correlation						
	County	**Locality**	**Surface area**	**Thick-max**	**Thick-median**	**Duration**
County		0.796	0.197	0.796	0.796	0.796
Locality	−0.105		1.000	0.014	0.142	0.142
Surface area	0.527	0.001*		1.000	1.000	1.000
Thickness (max)	−0.105	1.000	0.001*		0.142	0.142
Thickness (median)	−0.105	0.600	0.001*	0.600		0.014
Duration	−0.105	0.600	0.001*	0.600	1.000	

Table 2. Sampling variation of Cretaceous vertebrate fossils from Alabama. **Top**: Raw data of county numbers, Locality numbers, rock volume parameters (area and thickness), and duration. The duration is estimated based on the median of an approximate unit interval for each stratigraphic unit (Supplementary Fig. S1 left). **Bottom**: Results of Kendall's tau correlation. The numbers above the diagonal are the τ values, and the numbers below the diagonal are the p-values. An asterisk mark indicates a strongly correlated value. Data sources: [a]Based on a 1:250,000 state map. [b]Based on Raymond *et al.*[65]. [c]Soller (1995). [d]Supplimentary Fig. S1.

Results

An overview of 8,275 Cretaceous marine vertebrate specimens from Alabama is available in Ikejiri *et al.*[12]. Stratigraphic and geographic setting (Table 1; Supplementary Fig. S1) and relative taxonomic compositions based on specimen counts (Supplementary Tables S3 and S4) were first summarized. All 8,275 specimens came from 13 counties of central to western Alabama (surface area: approximately 160 × 50 km^2). They are housed at 12 institutions (listed in Supplementary Section 4). Of the 8,275 specimens, 3,301 specimens allowed the species-level identification with reliable stratigraphic information for this study. The sampling strategy (Table 2) and relative species richness based on rarefaction curves (Supplementary Fig. S3) and the Shareholder Quorum Subsampling (Fig. 2; Supplementary Table S2) are discussed below.

In total, 71 genera and 89 species of marine vertebrates were identified, including 17 uncertain species-level identification, from the five stratigraphic units: Unit 1 (lower Santonian) to Unit 5 (upper Maastrichtian) ranging from 86 to 66 million years ago (Supplementary Tables S3 and S4). Those Cretaceous marine vertebrates include 26 genera and 38 species of cartilaginous fishes (sharks, rays, and chimeras), 20 genera and 24 species of bony fishes (actinopterygians and a sarcopterygian), and 21 genera and 28 species of marine reptiles (mosasaurs, plesiosaurs, and sea turtles). Of the 89 species, 28 taxa represent a singleton status (i.e., 30.8% of the total species count) including 12 cartilaginous fish, five bony fish, and 11 reptilian species.

In the raw data with Lazarus occurrences, 89 species occurred 193 times (and 62 species with 155 occurrences in the data without singletons) in the five stratigraphic units. Of the five stratigraphic units, Unit 2 had the largest number of occurrences (n = 68 including singletons; n = 51 excluding singletons) (Supplementary Table S5). Those data indicate that the Early to Middle Campanian interval (Unit 2) represents the diversity peak of those marine vertebrates in northern Gulf of Mexico (Fig. 3). The least number of occurrences (n = 17 in the data with singletons) was found in Unit 4 (lower Maastrichtian). The Unit 5 (middle to upper Maastrichtian) also showed a considerably low number (n = 15 in the data without singletons). Those small numbers indicate that the diversity level was constantly low in the nearly entire Maastrichtian (Unit 4 and Unit 5). A declining diversity pattern appeared in Unit 3 to Unit 4 in the all vertebrate group and each of three subgroups, cartilaginous fish, bony fish, and marine reptiles.

Origination percentages were calculated in each time bin. The largest origination value occurred in Unit 1 (upper-most Santonian to lower Campanian) for all marine vertebrates in both types of the datasets with and without singletons (71.7% and 64.4% respectively) (Fig. 4; Supplementary Table S5). The origination percentages rapidly decreased at Unit 2 and maintained considerably low values from Unit 3 to Unit 5 as seen in the species count data. No marine vertebrate species originated (0.0%) in Unit 4. Those origination data suggest that diversity has remained noticeably low in through the nearly entire Maastrichtian for an approximately 8 million-year duration in this paleogeographic region.

Both including and excluding singleton data sets showed significantly high extinct species counts (higher than the upper 95% CIs) in Unit 2 for all vertebrates and the three subgroups (except for the marine reptiles without singletons setting) (Table 3; Supplementary Table S5). In the data with singletons, 40 marine vertebrate species disappeared while 25 was counted in the data without singletons. In all marine vertebrates, Unit 5 representing the latest Maastrichtian interval exhibited the second largest number of extinct species count. Each of the three subgroups, however, showed a slightly variable pattern of the count across the stratigraphic units. Overall, cartilaginous fish showed a considerably high number in Unit 5 (n = 9 with singletons; n = 5 without singletons),

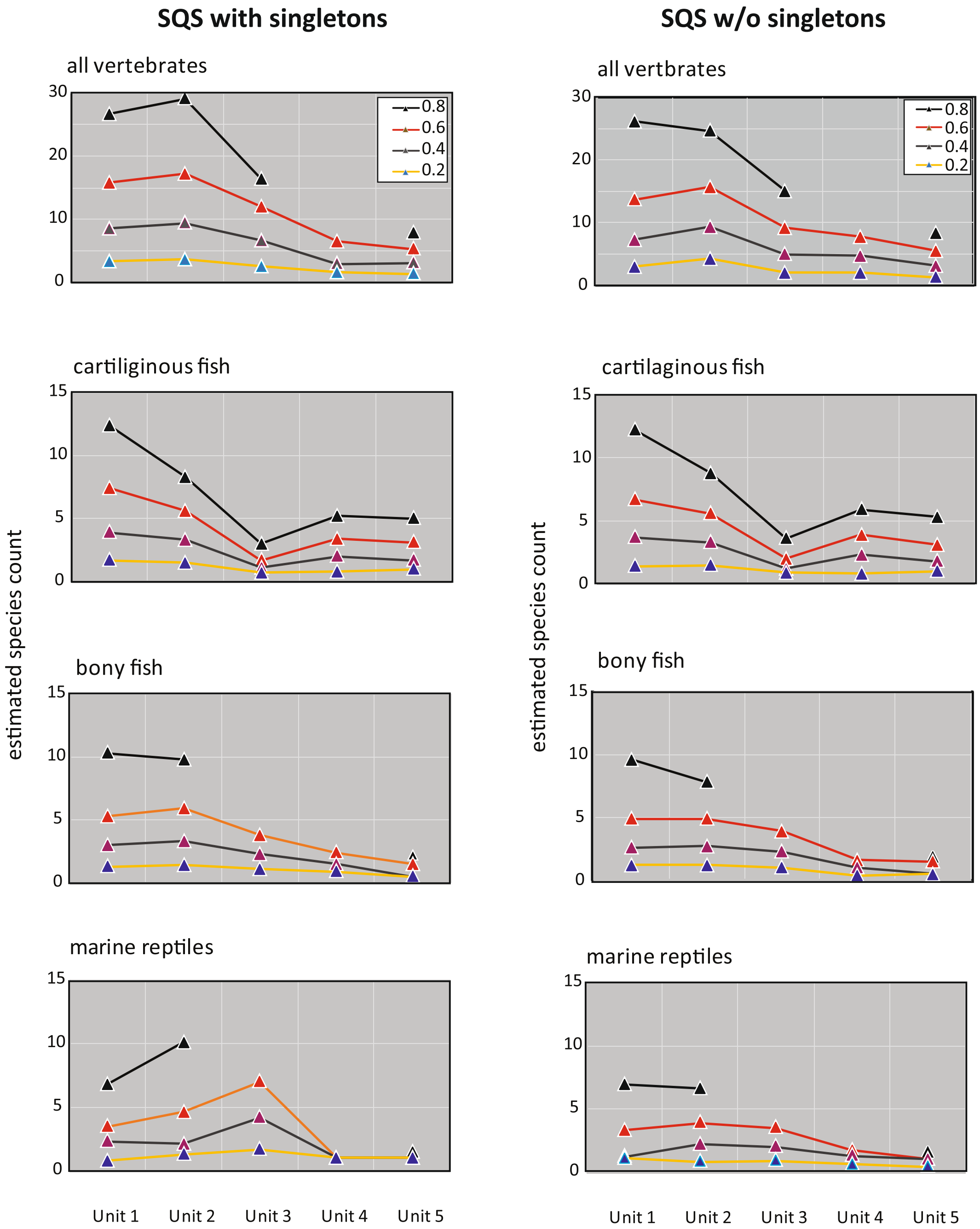


Figure 2. Subsample-level diversity of Late Cretaceous marine vertebrates from northern Gulf of Mexico. **Left**: including all taxa; **right**: excluding singletons. Standardized genus diversity is based on the shareholder quorum subsampling method by Alroy[17,76]. The quorum was set at 0.8, 0.6, 0.4, and 0.2 with 1,000 trials.

but bony fish and marine reptiles had an earlier declining signal in Unit 2 and Unit 3 (by the end of the Middle Campanian and around the Campanian–Maastrichtian boundary, respectively). At first glance, the extinct species counts suggest slightly different pathways of diversity loss among the three marine vertebrate groups.

While many marine vertebrate species disappeared just before the end-Maastrichtian (Unit 5), at least, three species survived through the K–Pg contact in northern Gulf of Mexico (Fig. 3; Supplementary Table S4). Those included the genus *Enchodus* (including two species *E. ferox* and *E. petrosus*: Aulopiformes) and *Cretalamna* (*C. appendiculata*: Lamniformes). Those K-Pg survivors may be considered as Dead Clade Walking (i.e., referring to extinction debt when a few still survive after a devastating event[16]). Based on the last occurrence data in Unit 5, possible victims around the K–Pg boundary were a few species of mosasaurs and protostegid turtles. Most lineages of rays (Myliobatiformes, Orectolobiformes, and Sclerorhynchiformes) and pycnodontiform bony fish also disappeared below the K–Pg. It is, however, worth noting that the magnitude of species declines could be greater in the earlier time (Unit 2 and/or Unit 3) than in the end-Maastrichtian extinction event (Unit 5). This

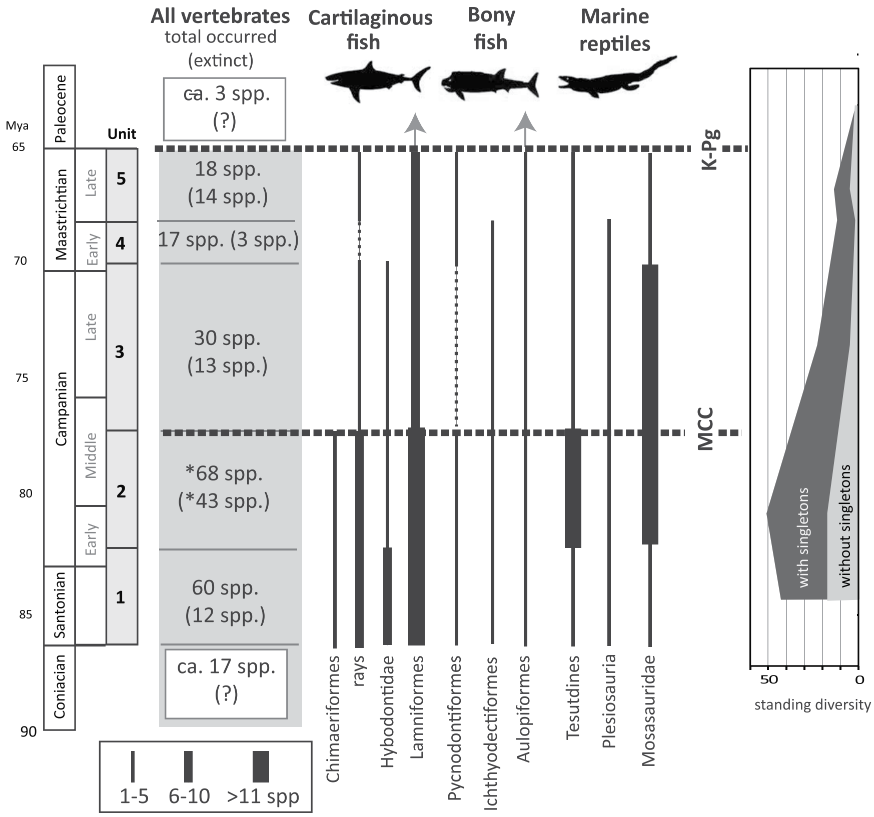


Figure 3. Biostratigraphic occurrence and diversity of Late Cretaceous marine vertebrates from northern Gulf of Mexico. Data show two major extinction events: Middle Campanian Crisis (MCC) and end-Maastrichtian (K–Pg) events. Standing diversity is calculated separately based on species counts with and without singletons.

earlier declining pattern is particularly applied for bony fishes and marine reptiles (see also other extinction values below).

Of all marine vertebrates, the largest and significantly high extinction percentage (Materials and Methods) was found in Unit 5 representing the K-Pg extinction based on the upper 95% CI (83.3% with singletons; 60.0% without singletons) (Fig. 4; Supplementary Table S5). Unit 2 in middle Campanian also showed considerably high extinction percentages in the two datasets, but no other units showed notably high values for all vertebrates. As seen in the extinct species counts, the cartilaginous fish and marine reptiles showed significantly high values in the latest Maastrichtian (Unit 5), but bony fish did not show any signs of devastation. Notably, in Unit 2 (lower to middle Campanian), the two fish groups exhibited high-level extinction pressure in both datasets. However, marine reptiles showed a moderate (in the singleton dataset) or very low extinction level. Only marine reptiles displayed a notably high extinction percentage in Unit 3 as also found in the species counts. Those data on the extinction percentage indicate that those marine vertebrates have different extinction patterns in the Late Cretaceous and multiple extinction events might occur such as in Unit 5 (i.e., the end-Maastrichtian) and Unit 2 (the end of middle Campanian) (Fig. 3).

Some common Late Cretaceous marine vertebrate taxa tend to have followed this overall extinction pathway – a combination of two large extinction impulses in Unit 2 (middle Campanian decline) and Unit 5 (late Maastrichtian to the K-Pg boundary). Those taxa specifically include chimeras, rays, hybodontid sharks (including Hybodontiforms and Ptychodontiformes), aulopiform fish, ichthyodectiform fish, and mosasaurs, based on extinction percentages (Table 3). Some other fish taxa, however, showed slightly different extinction pathways. For example, lamniform sharks showed a moderate-level extinction percentage in Unit 2. Then, they survived fairly well in Unit 3–Unit 4 and until hitting the major devastation in Unit 5. The single species of hybodontiform/ptychodontiform, *Ptychodus mortni*, might survive until Unit 3, but most of hybodontid and ptycodontod species disappeared by the end of Unit 2.

Different extinction patterns were also identified in the three marine reptiles, mosasaurs, sea turtles, and plesiosaurs. Many of those reptiles commonly exhibited a strong late Campanian declining trend (Unit 2 and Unit 3) based on a number of extinct species and the extinction percentages (Fig. 3; Table 3). In sea turtles including bothremydids, stem-basal chelonioids, and protostegids, while the highest extinction percentage appeared in Unit 2, they tend to have decreased continuously from Unit 2 to Unit 5. Plesiosaurs showed a very scatter fossil record from Alabama including an indeterminate elasmosaurid and polycotyrid taxa; Supplementary Table S3). The last occurrence of plesiosaurs is Unit 4, but no record of Unit 5 has been known. Mosasaurs have the 100% extinction rate at the K-Pg boundary but include only two species *Mosasaurus maximus* (cf. *M. hoffmani*) and

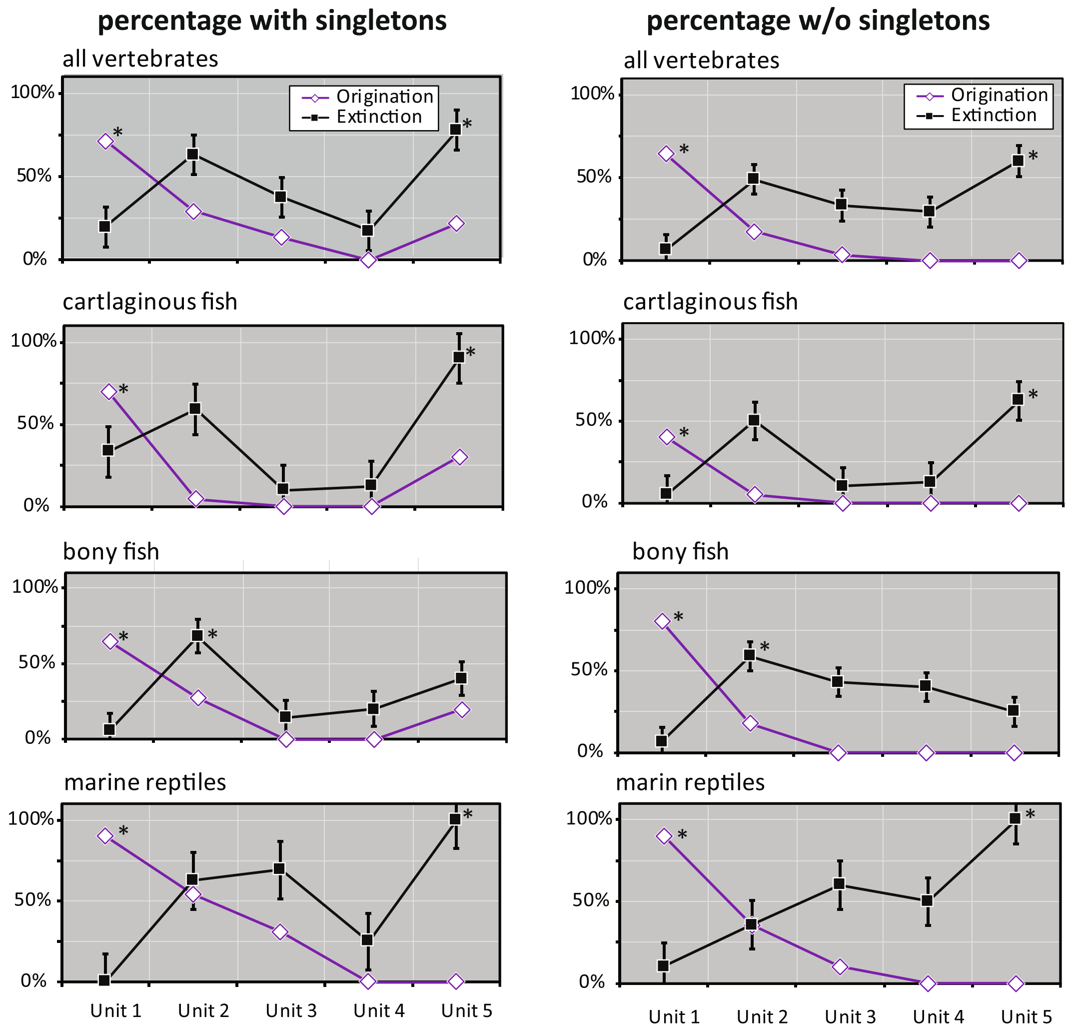


Figure 4. Origination (O) and extinction (E) percentages of Late Cretaceous marine vertebrates from northern Gulf of Mexico. Left: including all taxa; right: excluding singletons. The data used for this figure are listed in Supplementary Table S5. An asterisk mark indicates a significantly high percentage based on the upper 95 CI. Error bars of extinction percentage represent 95% confident intervals (following refs. [80,83]).

Plioplatecarpus sp. in Unit 5. The highest number of mosasaurs (n = 11) disappeared in middle Campanian (11 species in Unit 2 consisting of 63.3%), and this declining trend followed in later Campanian (57.1% in Unit 3).

Three types of extinction rates, proportional extinction (PE), proportional extinction rate per million years (PE m.y.), and per-capita extinction rate (q), were calculated solely based on the data excluding singletons (Materials and Methods). The two latter rates incorporate data of a duration of a time interval (stratigraphic unit) while the first one does not. In our dataset, the five stratigraphic units have a different duration ranging from approximately 2 to 8 million years (Table 2; Supplementary Fig. S1). Overall, the three types of rates of all vertebrates (Supplementary Table S6) showed a similar overall extinction pathway (i.e., a two-step diversity decline process in Unit 2 and Unit 5) as seen in the species count and extinction percentage (Fig. 4). In per-capita extinction rates (Fig. 5), the latest Maastrichtian (Unit 5) has the highest value, which is mainly based on cartilaginous fish. The highest value was also identified in Unit 2 for the all vertebrate and the two fish groups.

Discussion

Sampling effects and diversity comparisons. Diversity analyses for the fossil record cannot completely avoid the possibility of data distortion due to inconsistent fossil collecting (sampling), various conditions of preservation, different sedimentological settings, and so on[17]. To determine the risk of those kinds of potential biases, sampling variations and estimated species numbers generally provide some intuitions. In this study, six parameters of sampling variations in the duration in million years, fossil sites, and rock volume are compared (Table 2). Among those parameters, the surface area of each Formation (or Member) has the strongest tendency of correlation, especially, with the duration and relative strata thickness in the dataset. The numbers of localities (fossil sites) and counties (in Alabama) may contain a possible limitation (i.e., the largest number of fossil sites assigned to Unit 2), but other units tend to be constant.

Higher taxa	Key taxa	Specimen #s ([b])	Extinction percentage (%)					Extinct species count
			Unit 1	Unit 2	Unit 3	Unit 4	Unit 5	
Chimaeriformes	*Edaphodon*, *Ischyodus*	26	0.0	100.0*	0.0	0.0	0.0	4
rays[a]	*Borodinopristis*, *Brachyrhizodus*, *Pseudohypoliphus*	280	66.7	80.0*	50.0	0.0	100.0*	12
Hybodontiformes + Ptycodontiformes	*Ptychodus*, hybodontids	151	71.4	80.0	100.0	NA	NA	6
Lamniformes	*Cretalamina*, *Scapanorhynchus*, *Squalicorax*	1,243	16.7	27.3	0.0	0.0	85.7	13
Aulopiformes	*Enchodus*, *Stradodus*	857	0.0	33.3	25.0	25.0	33.3	3
Ichthyodectiformes	*Ichthyodectes*, *Xiphactinus*	244	0.0	50.0	50.0	100.0*	NA	4
Mosasauridae	*Clidastes*, *Mosasaurus*, *Tylosaurus*	1,563	0.0	63.6	57.1	0.0	100.0*	12
Testudines	*Ctenochelys*, *Protostega*, *Toxochelys*	1,250	0.0	54.5	60.0	50.0	100.0*	11
Plesiosauria	polycotylid sp., elasmosaurid sp.	56	0.0	33.3	50.0	100.0	NA	2

Table 3. Extinction selectivity for selected Late Cretaceous marine vertebrate groups from northern Gulf of Mexico. Extinction percentages of raw data are compared through the five-time bins. Numbers with an asterisk mark indicates a significantly high value. [a]Including Myliobatiformes, Orectolobiformes, Rajiformes, Sclerorhynchiformes, and Squatiniformes. [b]Data updated from Ikejiri *et al.*[12].

Regarding relative species richness, the rarefaction curves of all vertebrates and the three sub-vertebrate groups show a reasonably robust sample size in our dataset (Supplementary Figs. S3). The Shareholder Quorum Subsampling (SQS) at four different quora share similar overall topology of the diversity curve in all vertebrate and each of the three sub-groups (Fig. 2) (Supplementary Table S2). The highest diversity appears in Unit 2 and a continuous decline in Unit 3 to Unit 5 for all vertebrates. The three vertebrate subgroups, however, show slightly different patterns in the SQS curves. The evident difference appears in marine reptiles that exhibit the diversity peak at Unit 3. Cartilaginous and bony fish groups show similar diversity trends in overall, but a sharper decline occurs from Unit 2 to Unit 3 in the former group. Those different pathways of the three vertebrate subgroups reflect the real diversity pattern in our dataset. Otherwise, if our data are heavily distorted by different sampling strategies or preservational settings, all three groups will likely show the same pattern. In sum, we conclude that the data from the 3,301 vertebrate specimens is robust enough for further discussion of extinction patterns and processes.

With or without singleton taxa. Including or excluding singletons taxa has been an important issue for diversity analyses in the fossil record[18,19]. While many studies exclusively exclude singletons, some argue possible advantages for using taxa occurred in a single interval[20]. The extinction percentages of our marine vertebrate data show an overall similar extinction trend in both datasets with and without singletons (Fig. 4). However, the proportional and per-capita extinction rates of all vertebrates that exclude all singleton counts display a few notable differences among the three sub-vertebrate groups (Fig. 5; Supplementary Table S6). For example, marine reptiles have much smaller extinction rates in the latest Maastrichtian (Unit 5) than in the Campanian (Unit 2 and Unit 3). Also, bony fish does not show a decline signal in Unit 5 based on all extinction rates. Those patterns are largely not observed or not evident in the extinction percentages with the singleton data (Fig. 4).

We, thus, suggest that excluding singletons from our dataset possibly hide some important extinction signals or, at least, do not provide fine resolution to interpret the extinction trend. One of the reasons for the possible singleton effect is due to a relatively small number of time units (e.g., losing all bottom-boundary crossing taxa in Unit 1 when excluding singletons). Furthermore, some singleton taxa (listed in Supplementary Table S3) excluded in the all extinction rate analyses have a (relatively) high number of specimens[12]. This fact indicates that some or most singleton taxa in our dataset most likely represent a true diversity pattern (i.e., single time occurrence). Theoretically, finer biostratigraphic data from subdivided geologic units (e.g., Formation, Member) or strata-level occurrence can reduce a total singleton count in the dataset. This kind of approach must provide a better resolution of the extinction pattern although it is not practical at this moment. Therefore, we think that incorporating the two types of datasets is necessary for those marine vertebrates.

How many extinction events?. While 88 out of 90 marine vertebrate species became extinct for an over 20 million-year interval of the latest Cretaceous, two considerably large extinction events are recognized based on the data with singletons (Fig. 3). The largest extinction magnitude in all marine vertebrates is identified in Unit 5, which represents the end-Maastrichtian extinction event. Although extinct species counts are considerably low in Unit 5 (Supplementary Table S5), this extinction event had certainly impacted the marine vertebrate community near northern Gulf of Mexico. Of the three vertebrate groups, cartilaginous fish displays the severest devastation (Figs. 4 and 5). Bony fish and marine reptiles, however, do not show a strong signal of diversity loss. Different extinction pathways in the three vertebrate groups indicate a possible complex process with different causes toward the end-Maastrichtian.

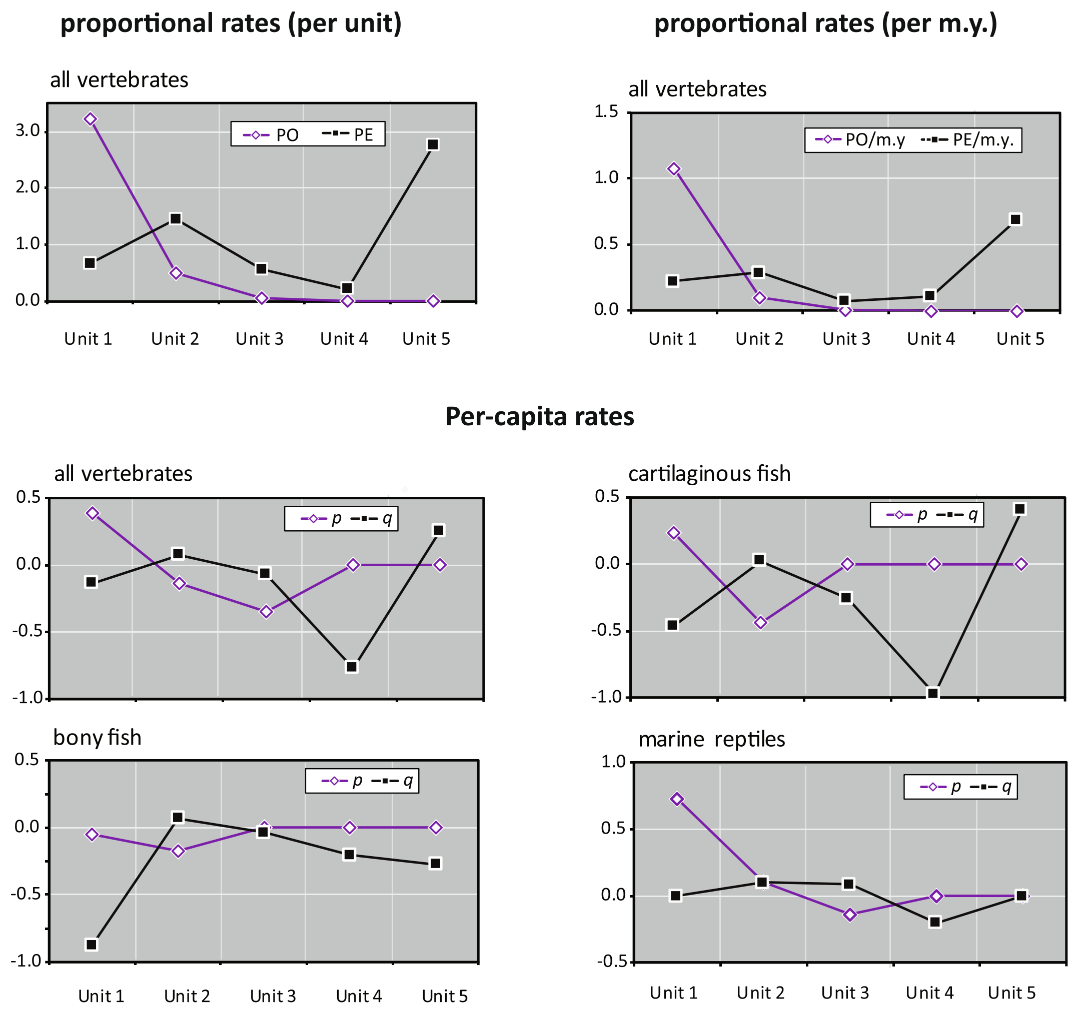


Figure 5. Origination and extinction rates of Late Cretaceous marine vertebrates from northern Gulf of Mexico. Three types of rates are compared based on data without singletons, including PO (proportional origination), PE (proportional extinction), p (per-capita origination), and q (per-capita extinction) (see Materials and Methods). The original data and other kinds of extinction rates are available in Supplementary Table S6.

Another large extinction event is identified in Unit 2 during the Middle Campanian (Fig. 3). This 'Middle Campanian Crisis' event is characterized by a combination of significantly high diversity and a sharp decline in the time interval (Figs. 4 and 5). The two fish groups tend to be involved more explicitly than marine reptiles. In particular, bony fish has the largest extinction magnitude through the five Late Cretaceous units. In marine reptiles, some species also disappeared during the Middle Campanian Crisis, but the majority of mosasaurs, plesiosaurs, and sea turtles have vanished in the Late Campanian to the earliest Maastrichtian (Unit 3) in northern Gulf of Mexico.

Many studies on marine vertebrate extinctions have emphasized the end-Maastrichtian event (e.g., marine reptiles[4,6,8], mosasaurs[7], plesiosaurs[21], sharks[11], bony fish[5]) while a few studies have also pointed out the possibility of Campanian extinctions (e.g., actinopterygian and mosasaur fauna in Sweden[22,23]). Our study suggests that species-level data from a selected geographic region have some advantages to reveal the Middle Campanian biodiversity loss. In contrast to Cretaceous marine vertebrates, some studies of marine invertebrates and plankton show signals of a large extinction magnitude that can be referred to as the Middle Campanian Crisis. For example, some mollusks show evident declined patterns in the Middle to Late Campanian (e.g., ammonites[24–28], gastropods[29], inoceramids[30,31], rudists[32], a combination of various taxa[33,34]). In marine plankton, some studies display continuous background extinctions throughout the Campanian (e.g., nannoplankton[35,36], foraminifera[37,38]).

Near the northern Gulf of Mexico region, detailed extinction patterns have not been well known for most Cretaceous marine taxa. A few previous studies on mollusks[39] and plankton[40] cover only selected layers of the upper-most Maastrichtian formations (i.e., the upper part of Unit 5), but no published data are available for the Campanian and early Maastrichtian records. Hypothetically, non-vertebrate marine taxa may have a different extinction pathway from marine vertebrates since due to various types of paleoecological (e.g., life habitats and modes, relative trophic level positions) and biological factors (e.g., species longevity, body size)[41,42]. To further investigate this hypothetical scenario, data of strata- or layer-based fossil occurrence for selected taxa will be necessary.

Local vs. global phenomena?. Could this Middle Campanian Crisis be paleogeographically a global phenomenon for the marine ecosystem? To date, no comprehensive data to outline spatial extinction patterns of all marine vertebrates are available in the literature. We have attempted to investigate the Middle Campanian Crisis in global-scale data of marine vertebrates in the Paleobiology Database (Supplementary Tables S7 and S8). As for a reference, a total of 396 genera of marine vertebrates recorded from five intervals, using an 8 million-year time bin for each, from the Cenomanian to the end of the Paleocene (about 40.1 million years in total duration) occur 690 times in total. The genus-level based global data show the largest extinction percentage (57.2%: Supplementary Table S7) at the latest Cretaceous time bin for all vertebrates, cartilaginous fish, and marine reptiles.

There are difficulties to draw a clear conclusion of whether the Middle Campanian Crisis involved marine vertebrates on a global scale. The main reason is that many taxa in the dataset exhibit uncertainty in alpha taxonomy at the species-level identification and even in higher-levels (e.g., family, order). Those include some major or relatively common Cretaceous marine vertebrate taxa, specifically assigned to rays, lamniforms, crossognathiforms, ichthyodectiforms, tselfatiforms, and sea turtles. Another challenge in using global data lies in the limitation of the stratigraphic setting. The database does not provide robust data to extract a time interval that matches the Middle Campanian for quantitative comparisons with our data. Thus, we suggest that the global data of Cretaceous marine vertebrates presented here is a reference for general information and further analysis of the global data for detailed diversity patterns is needed (currently under study by one of the authors, T. I.).

Potential cause(s) of the middle campanian crisis. Of the two extinction events of Late Cretaceous marine vertebrates in northern Gulf of Mexico, the Chicxulub impact is likely the strongest candidate for the main cause of the latest Maastrichtian devastation[43,44] (Supplementary Fig. S2). Many studies reveal a series of aftermath global marine environmental changes triggered by the impact, such as impact bursts[45], mega-tsunami[46,47], and climate changes[48–51]. Since Alabama is physically located merely 500 km away from the impact site (Fig. 1), this catastrophic event likely affected the 12 species that disappeared during the time of Unit 5, and as the result, iconic Cretaceous marine vertebrates, mosasaurs, sea turtles, a few groups of rays, and possibly lamniform sharks were completely wiped off from the Gulf of Mexico.

Determining the main physical cause(s) of the Middle Campanian Crisis is more challenging for the marine vertebrate community. To our knowledge, the globally impactful event at the corresponding time and space is uncertain. Some kinds of global long-term marine environmental changes in the Late Cretaceous, however, can be considered as possible candidates. Those include, for example, sea-level change (esp., global regression[52–55]), faunal change in plankton[40], marine anoxia[56], ocean acidification[49,57–59], and the Strangelove oceans[58,60]. Among those hypotheses for a global scale, circumstantial evidence from northern Gulf of Mexico indicates a series of regression events (e.g., refs. [61,62]) that must affect marine vertebrate diversity to some degree (Supplementary Fig. S4). Moreover, an alternative possibility is a relatively large asteroid impact in central Alabama. The Wetumpka Impact crater, exhibiting 7.6 km in diameter, is estimated to occur sometime in the time of the Mooreville Chalk (Unit 2: ca. Early to Middle Campanian)[63]. To further investigate this hypothetical scenario, more precise data on the impact age and magnitude will be needed.

Materials and Methods

Geologic setting. Following Ikejiri *et al.* (ref. [12]), Upper Cretaceous geologic units (a combination of formations and members) were subgrouped into five successive stratigraphic units (Table 1; Supplementary Table S1). Surface rocks of those Cretaceous units are geographically distributed in the mid-region from northwestern to central-eastern Alabama (Supplementary Fig. S1). Surface area data of each unit are available in the USGS Geologic maps of US states (ref. [64] accessed on July 2016). Ages of the geologic formations and members are based on ref. [65] and USGS Geolex[66]. Using a Formation- and Member-based time setting can provide finer intervals than numerical values (e.g., 10 million-year) when determining extinction and diversity patterns[67]. The five successive units used in this study exhibited approximately 20 million- year total duration, which consists of about a 4 million-year bin for each unit. Most of the marine vertebrate fossils from Alabama do not have layer- or strata-level stratigraphic information.

In Alabama, an unconformity might occur twice in the upper Cretaceous units: in the contact of the Prairie Bluff Chalk (upper Maastrichtian) – the Clayton Formation (lower Paleogene) and within the Reply Formation (lower Maastrichtian). Those unconformities can be arguable and may occur only regionally (e.g., refs. [13,68]). In the K–Pg contact between the upper Maastrichtian Prairie Bluff Chalk and the Paleogene Clayton Formation (Supplementary Fig. S2), nannoplankton data indicate a regional unconformity ranging from 0.4 million to possibly over a few million years[69–71]. Strontium isotope and paleomagnetism, however, suggests a successive K–Pg boundary with no unconformity[39,72]. Possible tsunami deposits with direct impact materials (e.g., impact ejecta, glass spherules, microtektites) have been reported from several K–Pg sites near the Mississippi Embayment[71]. During a series of field investigations, we found typical Late Cretaceous taxa, such as the lamniform shark (*Squalicorax*) and mosasaur (cf. *Mosasaurus*), from the base of the Paleogene Clayton Formation (Supplementary Fig. S2 and Table S4). These data may represent a reworked condition (as suggested by refs. [61,62]) although further investigation seems to be needed for verification.

Sampling variations and subsampling. For sampling variations (following refs. [73,74]), we used a correlation test to compare the relation of six sampling measures, such as (1) counties, (2) fossil localities, (3) the surface area of each geologic unit, (4) maximum and (5) median of each unit, and (6) a duration (my) for each stratigraphic unit. We used Kendall's tau due to expecting a non-linear relation in the dataset. The PAST (version 2.08[75])was used to run rarefaction analysis. Relative fossil richness was estimated by the Shareholder Quorum Subsampling; the quorum, μ, was set as 0.2, 0.4, and 0.8 for comparisons with a total of 1000 subsampling trials for each dataset (using the R code provided by ref. [17]). For this analysis, using 'two timmers' species counts (N_{2t}; ref. [76]) was applied for specimens with reliable species-level identification when genera consist of multiple taxa. The result is shown in Fig. 3.

Marine vertebrate fossils. Data on species counts were collected only from museum specimens that are officially curated (by the summer of 2015). Twelve institutions in the U.S. and U.K. store those specimens (Supplementary Materials Section 4). In total, over 8,275 specimens were stored in the institutions, and only ones with reliable generic level identification with valid stratigraphic information (n = 6,352) were selected for this study (Supplementary Table S3). The taxonomic status was checked mostly in actual specimens by the author (T.I.), and some results were reported[11]. The 6,352 specimens include a mix of specimens with skeletons and isolated bones that exhibited enough proportions to examine certain morphologies. Of Cretaceous vertebrate fossils from Alabama, only fully aquatic forms were scoped in this study, including cartilaginous fishes (sharks, rays, sawfish, and chimeras), bony fishes (actinopterygians and sarcopterygian fish), and marine reptiles (mosasauroid squamates, plesiosaur sauropterygians, and chelonioid testudines). Semiaquatic and fully terrestrial archosaurs, such as crocodilians, pterosaurs, non-avian dinosaurs, and birds, were not included (those excluded taxa are listed in ref. [12]. Only specimens with bony tissues, such as skeletons, bones, and teeth, were analyzed, but scale-specimens for some fish taxa (e.g., refs. [77,78]) were not included.

Global data of Late Cretaceous marine vertebrates were downloaded from the Paleobiology Database[79] (http://fossilworks.org; accessed in August 2019). Stratigraphic and geographic occurrences were chosen for quantitative comparisons at the genus-level because species-level taxonomic assignments and occurrences may contain more uncertainties.

Data quantification for extinction patterns. Supplementary Tablesbiting a singleton status (i.e., species occurred only in a single geologic unit) can yield a large amount of important information to assess extinction patterns and processes as suggested by two studies[80,81], and those taxa were, thus, included for this study. However, data excluding singletons were also analyzed for comparison. Since there is a hiatus in the earlier Santonian (below Unit 1) in Alabama, occurrence of some species in Unit 0 (Supplementary Table S3) were based on the record from other areas of the Gulf of Mexico or the Western Interior Seaway Lazarus taxa that occurred 22 times in 13 species (seven times in Unit 3 and nine in Unit 4, and once in Unit 5) were included for all data analyses. For calculating origination (O) and extinction (E) percentages, total species counts (N) per time bin (Stratigraphic Unit) were used as O/N and E/N for the data set with and without singletons. Various extinction and origination rates with boundary-crossing measures such as (1) proportional (PE and PO), (2) proportional rate per m.y., and (3) per-capita rates (p and q), analyzed for this study followed refs. [18,19].

Received: 3 July 2019; Accepted: 14 February 2020;
Published online: 06 March 2020

References

1. Raup, D. M. & Sepkoski, J. J. Mass extinctions in the marine fossil record. *Science* **215**, 1501–1503, https://doi.org/10.1126/science.215.4539.1501 (1982).
2. Raup, D. M. *Extinction: Bad Genes or Bad Luck?* W. W. Norton & Company. 224 p. (1991a).
3. Bambach, R. K., Bush, A. M. & Erwin, D. H. Autecology and the filling of ecospace–key metazoan radiations. *Palaeontology* **50**, 1–22, https://doi.org/10.1111/j.1475-4983.2006.00611.x (2007).
4. Bardet, N. Extinction events among Mesozoic marine reptiles. *Hist. Biol.* **7**, 313–324, https://doi.org/10.1080/10292389409380462 (1994).
5. Friedman, M. Explosive morphological diversification of spiny-finned teleost fishes in the aftermath of the end-Cretaceous extinction. *Proc. R. Soc. B* **277**, 1675–1683, https://doi.org/10.1098/rspb.2009.2177 (2010).
6. Benson, R. B. J., Butler, R. J., Lindgren, J. & Smith, A. S. Mesozoic marine tetrapod diversity: mass extinctions and temporal heterogeneity in geological megabiases affecting vertebrates. *Proc. R. Soc. B* **277**, 829–834, https://doi.org/10.1098/rspb.2009.1845 (2009).
7. Polcyn, M., Jacobs, L. L., Araujo, R., Schulp, A. S. & Mateus, O. Physical drivers of mosasaur evolution. *Palaeogeogr. Palaeoclimatol. Palaeoecol.* **400**, 17–27, https://doi.org/10.1016/j.palaeo.2013.05.018 (2014).
8. Fischer, V., Bardet, N., Benson, R. B. J., Arkhangelsky, M. S. & Friedman, M. Extinction of fish-shaped marine reptiles associated with reduced evolutionary rates and global environmental volatility. *Nat. Commun.* **7**, 10825, https://doi.org/10.1038/ncomms10825 (2016).
9. Gallagher, W. B. Selective extinction and survival across the Cretaceous/Tertiary boundary in the northern Atlantic Coastal Plain. *Geology* **19**, 967–970, https://doi.org/10.1130/0091-7613(1991)019<0967:SEASAT>2.3.CO2 (1991).
10. Belben, R. A., Underwood, C. J., Johanson, Z. & Twitchett, R. J. Ecological impact of the end-Cretaceous extinction on lamniform sharks. *PLoS ONE* **12**(6), e0178294, https://doi.org/10.1371/journal.pone.0178294 (2017).
11. Bazzi, M., Kear, B. P., Blom, H., Ahlberg, E. & Campione, N. E. Static dental disparity and morphological turnover in sharks across the end-Cretaceous mass extinction. *Curr. Biolo.* **28**, 2607–2615.e3, https://doi.org/10.1016/j.cub.2018.05.093 (2018).
12. Ikejiri, T., Ebersole, J., Blewitt, H. L. & Ebersole, S. An overview of Late Cretaceous vertebrates from Alabama. *Ala. Mus. Nat. Hist. Bull.* **31**(1), 46–71 (2013).
13. Mancini, E. A., Puckett, T. M., Tew, B. H. & Smith, C. C. Upper Cretaceous sequence stratigraphy of the Mississippi – Alabama area. *Gulf Coast. Assoc. Geolo. Soc. Trans.* **45**, 377–384 (1995).
14. Ebersole, J. A. & Dean, L. The history of Late Cretaceous vertebrate research in Alabama. *Ala. Mus. Nat. Hist. Bull.* **31**(1), 3–45 (2013).
15. Ikejiri, T. & Everhart, M. J. Notes on the Authorship and Holotype of Ptychodus mortoni (Chondrichthyes, Ptychodontidae). *N. Mexico Mus. Nat. Sci. Bull.* **67**, 69–73 (2015).
16. Jablonski, D. Survival without recovery after mass extinctions. *Proc. Natl. Acad. Sci. USA* **99**, 8139–8144, https://doi.org/10.1073/pnas.102163299 (2002).

17. Alroy, J. Geographical, environmental and intrinsic biotic controls on Phanerozoic marine diversification. *Palaeontology* **53**, 1211–1235, https://doi.org/10.1111/j.1475-4983.2010.01011.x (2010a).
18. Foote, M. Origination and extinction components of taxonomic diversity: general problems. Paleobiology **26** (**sp4**) 74–102, https://doi.org/10.1666/0094-8373(2000)26[74:OAECOT]2.0.CO2 (2000).
19. Foote, M. & Miller, A. I. *Principles of Paleontology Third Edition*. W. H. Freeman and Company, 354 pp (2007).
20. Cascales-Miñana, B. & Diez, J. B. The effect of singletons and interval length on interpreting diversity trends from the palaeobotanical record. *Palaeontol. Electron*. **15**, 6A https://palaeo-electronica.org/content/2012-issue-1-articles/123-palaeofloristic-patterns (2012).
21. Bakker, R. T. Plesiosaur extinction cycles- Events that mark the beginning, middle and end of the Cretaceous. *Geol. Assoc. Can. Spec. Pap.* **39**, 641–664 (1993).
22. Bazzi, M., Einarsson, E. & Kear, B. P. Late Cretaceous (Campanian) actinopterygian fishes from the Kristianstad Basin of southern Sweden. *Geol. Soc., London, Spec. Publ.* **434**, 277–292, https://doi.org/10.1144/SP434.5 (2016).
23. Lindgren, J. Stratigraphical distribution of Campanian and Maastrichtian mosasaurs in Sweden – evidence of an intercontinental marine extinction event? *GFF* **126**, 221–229, https://doi.org/10.1080/11035890401262221 (2004).
24. Hancock, J. M. Some Cretaceous-Tertiary marine faunal changes, *In* Harland, W. B. *et al.* eds. *The Fossil Record*. London, Geological Society of London, 91–104 (1967).
25. Wiedmann, J. Evolution or revolution of ammonoids at Cretaceous system boundaries. *Biol. Rev.* **48**, 159–194, https://doi.org/10.1111/j.1469-185X.1973.tb00979.x (1973).
26. Kennedy, W. J. Ammonite evolution, *In* Hallam, A. ed. *Patterns of Evolution. Amsterdam*, Elsevier Scientific Publishing Co., 251–304 (1977).
27. Ward, P. D. & Signor, P. W. Evolutionary tempo in Jurassic and Cretaceous ammonites. *Paleobiology* **9**, 183–198, https://doi.org/10.1017/S0094837300007569 (1983).
28. Jagt-Yazykova, E. A. Palaeobiogeographical and palaeobiological aspects of mid- and Late Cretaceous ammonite evolution and bio-events in the Russian Pacific. *Scr. Geologica* **143**, 15–121 (2011).
29. Ruban, D. A. Were Late Cretaceous extinctions of gastropods selective by generic longevity? *Geosci. Front.* **4**, 87–93, https://doi.org/10.1016/j.gsf.2012.04.002 (2013).
30. Dhondt, A. V. Cretaceous inoceramid biogeography–a review. *Palaeogeogr. Palaeoclimatol. Palaeoecol.* **92**, 217–232, https://doi.org/10.1016/0031-0182(92)90083-H (1992).
31. Crame, J. A. & Luther, A. The last inoceramid bivalves in Antarctica. *Cretac. Res.* **18**, 179–195, https://doi.org/10.1006/cres.1996.0055 (1997).
32. Johnson, C. C. The rise and fall of rudist reefs. *Am. Sci.* **90**(2), 148–153 (2002).
33. Kauffman, E. G. *et al*. Molluscan biostratigraphy of the Cretaceous Western Interior Basin, North America. *Geol. Assoc. Can. Spec. Pap.* **39**, 435–451 (1993).
34. Marshall, C. R. & Ward, D. Sudden and gradual molluscan extinctions in the Latest Cretaceous of western European Tethys. *Science* **274**, 360–1363, https://doi.org/10.1126/science.274.5291.1360 (1996).
35. Jiang, S., Bralower, T. J., Patzkowsky, M., Kump, L. R. & Schueth, J. D. Geographic controls on nannoplankton extinction across the Cretaceous/Palaeogene boundary. *Nat. Geosci.* **3**, 80–285, https://doi.org/10.1038/ngeo775 (2010).
36. Melinte, M. C. & Jipa, D. Campanian–Maastrichtian marine red beds in Romania: biostratigraphic and genetic significance. *Cretac. Res.* **26**, 49–56, https://doi.org/10.1016/j.cretres.2004.11.002 (2005).
37. D'Hondt, S. L., Herbert, T. D., King, J. & Gibson, C. Planktonic foraminifera, asteroid, and marine production–death and recovery at the Cretaceous-Tertiary boundary. *Geol. Soc. Am. Spec. Pap.* **307**, 303–317, https://doi.org/10.1130/0-8137-2307-8.303 (1996).
38. Alegret, L., Thomas, E. & Lohmann, K. C. End-Cretaceous marine mass extinction not caused by productivity collapse. *Proc. Nat. Acad. Sci. USA* **109**, 728–732, https://doi.org/10.1073/pnas.1110601109 (2012).
39. Bryan, J. R. & Jones, D. S. Fabric of the Cretaceous-Tertiary marine macrofaunal transition at Braggs, Alabama. *Palaeogeogr. Palaeoclimatol. Palaeoecol.* **69**, 279–301, https://doi.org/10.1016/0031-0182(89)90170-3 (1989).
40. Mancini, E. A., Tew, B. H. & Smith, C. C. Cretaceous-Tertiary contact, Mississippi and Alabama. *J. Foraminifer. Res.* **19**, 93–104 (1989).
41. Sogot, C. E., Harper, E. M. & Taylor, D. Biogeographical and ecological patterns in bryozoans across the Cretaceous-Paleogene boundary: Implications for the phytoplankton collapse hypothesis. *Geol.* **41**, 631–634, https://doi.org/10.1130/G34020.1 (2013).
42. Kennedy, W. J. Thoughts on the evolution and extinction of Cretaceous ammonites. *Proc. Geol. Assoc.* **100**(3), 251–279, https://doi.org/10.1016/S0016-7878(89)80047-1 (1989).
43. Alvarez, L. W., Alvarez, W., Asaro, F. & Helen, M. V. Extraterrestrial cause for the Cretaceous-Tertiary extinction. *Science* **208**, 1095–1108, https://doi.org/10.1126/science.208.4448.1095 (1980).
44. Schulte *et al*. The Chicxulub asteroid impact and mass extinction at the Cretaceous-Paleogene boundary. *Science* **327**, 1214–1218, https://doi.org/10.1126/science.1177265 (2010).
45. Denne, R. A. *et al*. Massive Cretaceous-Paleogene boundary deposit, deep-water Gulf of Mexico. New evidence for widespread Chicxulub-induced slope failure. *Geol.* **41**, 983–986, https://doi.org/10.1130/G34503.1 (2013).
46. Matsui, T., Imamura, R., Tajika, E., Nakano, Y. & Fujisawa, Y. Generation and propagation of a tsunami from the Cretaceous-Tertiary impact event. *Geol. Soc. Am. Spec. Pap.* **356**, 69–77, https://doi.org/10.1130/0-8137-2356-6.69 (2002).
47. Campbell, C. E., Oboh-Ikuenobe, F. E. & Eifert, T. L. Megatsunami deposit in Cretaceous-Paleogene boundary interval of southeastern Missouri, *in* Evans, K. R., Horton, J. W. Jr. King, D. T. Jr. & Morrow, J. R. eds., The Sedimentary Record of Meteorite Impacts. *Geol. Soc. Am. Spec. Pap.* **437**, 189–198, https://doi.org/10.1130/2008.2437(11) (2008).
48. Renne, R. *et al*. Time scales of critical events around the Cretaceous-Paleogene boundary. *Science* **339**, 684–687, https://doi.org/10.1126/science.1230492 (2013).
49. Ohno, S., Konfo, T. & Sugita, S. Production of sulphate-rich vapor during the Chicxulub impact and implication for ocean acidification. *Nat. Geosci.* **7**, 279–282, https://doi.org/10.1038/ngeo2095 (2014).
50. Vellekoop, J. *et al*. Rapid short-term cooling following the Chicxulub impact at the Cretaceous–Paleogene boundary. *Proc. Nat. Acad. Sci. USA* **111**, 7537–7541, https://doi.org/10.1073/pnas.1319253111 (2014).
51. Tyrrell, T., Merico, A., Armstrong, M. & McKay, D. I. A. Severity of ocean acidification following the end-Cretaceous asteroid impact. *Proc. Nat. Acad. Sci. USA* **112**, 6556–6561, https://doi.org/10.1073/pnas.1418604112 (2015).
52. Haq, B. U., Hardenbol, J. & Vail, R. Mesozoic and Cenozoic chronostratigraphy and cycles of sea-level change. *SEPM Spe. Publ.* **42**, 71–108, https://doi.org/10.2110/pec.88.01.0071 (1988).
53. Jablonski, D. & Raup, D. M. Selectivity of end-Cretaceous marine bivalve extinctions. *Science* **268**, 389–391, https://doi.org/10.1126/science.11536722 (1995).
54. Dhondt, A. V., Malchus, N., Boumaza, L. & Jaillard, E. Cretaceous oysters from North Africa; origin and distribution. *Bull. Soc. Geol. Fr.* **170**(1), 67–76 (1999).
55. Peters, S. E., Kelly, D., Fraass, C. & Andrew, J. Oceanographic controls on the diversity and extinction of planktonic foraminifera. *Nat.* **493**, 398–401, https://doi.org/10.1038/nature11815 (2013).
56. Turgeon, S. C. & Creaser, R. A. Cretaceous oceanic anoxic event 2 triggered by a massive magmatic episode. *Nat.* **454**, 323–326, https://doi.org/10.1038/nature07076 (2008).

57. D'Hondt, S., Pilson, M. E. Q., Sigurdsson, H., Hanson, A.K. Jr. & Carey, S. Surface-water acidification and extinction at the Cretaceous-Tertiary boundary. *Geology* **22**, 983–986, https://doi.org/10.1130/0091-7613(1994)022%3C0983:SWAAEA%3E2.3.CO;2 (1994).
58. Canfield, D. E. A new model for Proterozoic ocean chemistry. *Nat.* **396**, 450–453, https://doi.org/10.1038/24839 (1998).
59. Hönisch, B. *et al*. The geological record of ocean acidification. *Sci.* **335**, 1058–1063, https://doi.org/10.1126/science.1208277 (2012).
60. Kump, L. R. Interpreting carbon-isotope excursions. strangelove oceans. *Geology* **19**, 299–302, https://doi.org/10.1130/0091-7613(1991)019%3C0299:ICIESO%3E2.3.CO;2 (1991).
61. Hart, M. B., Harries, J. & Cárdenas, A. L. The Cretaceous/Paleogene boundary events in the Gulf Coast–Comparisons between Alabama and Texas. *Gulf Coast. Assoc. Geolo. Soc. Trans.* **63**, 235–255 (2013).
62. Hart, M. B., FitzPatrick, M. E. J. & Smart, C. W. The Cretaceous/Paleogene boundary. foraminifera, sea grasses, sea level change and sequence stratigraphy. *Palaeogeogr. Palaeoclimatol. Palaeoecol.* **441**, 420–429, https://doi.org/10.1016/j.palaeo.2015.06.046 (2016).
63. King, D. T. Jr., Morrow, J. R., Petruny, L. W. & Ormö, J. Surficial polymict impact breccia unit, Wetumpka impact structure, Alabama. Shock levels and emplacement mechanism. *Geol. Soc. Am. Spec. Pap.* **518**, 149–164, https://doi.org/10.1130/2015.2518(10) (2015).
64. Horton, J. D. The State Geologic Map Compilation (SGMC) geodatabase of the conterminous United States (ver. 1.1, August 2017): U.S. Geological Survey data release, https://mrdata.usgs.gov/geology/state/ (2017)
65. Raymond, D. E., Osborne, W. E., Copeland, C. W. & Neathery, T. L. Alabama Stratigraphy. *Geol. Surv. Ala. Cir.* **40**, 1–97 (1988).
66. Soller, D. Geolex – National Geologic Map – USGS, https://ngmdb.usgs.gov/Geolex/search (2005).
67. Peters, S. E. & Foote, M. Biodiversity in the Phanerozoic: a reinterpretation. *Paleobiology* **27**, 583–601, https://doi.org/10.1666/0094-8373(2001)027%3C0583:BITPAR%3E2.0.CO;2 (2001).
68. Worsley, T. The Cretaceous-Tertiary boundary event in the ocean. *Soc. Econ. Paleontol. Mineral.* **20**, 90–125, https://doi.org/10.2110/pec.74.20.0094 (1974).
69. Donovan, D. *et al*. Sequence stratigraphic setting of the Cretaceous-Tertiary boundary in central Alabama. *Soc. Econ. Paleontol. Mineral.* **42**, 299–307, https://doi.org/10.2110/pec.88.01.0299 (1988).
70. Smith, C. C. The Cretaceous-Tertiary boundary at Moscow Landing, west-central Alabama. *Geol. Surv. Ala. Repr.* **112**, 533–539 (1997).
71. Keller, G. *et al*. Chicxulub impact spherules in the North Atlantic and Caribbean: age constraints and Cretaceous-Tertiary boundary hiatus. *Geolo. Mag.* **150**, 885–907, https://doi.org/10.1017/S0016756812001069 (2013).
72. Jones, D. S. *et al*. Biotic, geochemical, and paleomagnetic changes across the Cretaceous/Tertiary boundary at Braggs, Alabama. *Geology* **15**, 311–315, https://doi.org/10.1130/0091-7613(1987)15%3C311:BGAPCA%3E2.0.CO;2 (1987).
73. Dunhill, A. M., Benton, M. J., Twitchett, R. J. & Newell, A. J. Testing the fossil record: Sampling proxies and scaling in the British Triassic–Jurassic. *Palaeogeogr. Palaeoclimatol. Palaeoecol.* **404**, 1–11, https://doi.org/10.1016/j.palaeo.2014.03.026 (2014).
74. Walker, F. M., Dunhill, M. A., Woods, M. A., Newell, A. J. & Benton, M. J. Assessing sampling of the fossil record in a geographically and stratigraphically constrained dataset: the Chalk Group of Hampshire, southern UK. *J. Geol. Soc.* **174**, 509–521, https://doi.org/10.1144/jgs2016-093 (2017).
75. Hammer, Ø., Harper, D. A. T. & Ryan, P. D. 2001. PAST: paleontological statistics software package for education and data analysis. *Paleontol. Electron.* **4**(1), 9 https://palaeo-electronica.org/2001_1/past/issue1_01.htm (2001).
76. Alroy, J. Fair sampling of taxonomic richness and unbiased estimation of origination and extinction rates. *Paleontol. Soc. Pap.* **16**, 55–80, https://doi.org/10.1017/S1089332600001819 (2010b).
77. Applegate, S. P. The vertebrate fauna of the Selma Formation of Alabama. *Fieldiana Geol. Mem.* **3**, 385–433 (1970).
78. Thurmond, J. T. & Jones, D. E. Fossil Vertebrates of Alabama: Tuscaloosa, University of Alabama Press, 244 p. (1981).
79. Carrano, M.T. *et al*. Taxonomic occurrences of Cretaceous to Paleocene Vertebrata recorded: *In*: Fossilworks, the Evolution of Terrestrial Ecosystems database, and the Paleobiology Database, http://fossilworks.org (2016).
80. Benton, M. J., Tverdokhlebov, P. & Surkov, M. V. Ecosystem remodeling among vertebrates at the Permian–Triassic boundary in Russia. *Sci.* **432**, 97–100, https://doi.org/10.1038/nature02950 (2002).
81. Stanley, S. M. Estimates of the magnitudes of major marine mass extinctions in earth history. *Proc. Nat. Acad. Sci. USA* **113**, 6325–6334, https://doi.org/10.1073/pnas.1613094113 (2016).
82. Scotese, C. R. Atlas of Late Cretaceous Paleogeographic Maps, PALEOMAP Atlas for ArcGIS, volume 2, The Cretaceous, Maps 16 – 22, Mollweide Projection, PALEOMAP Project, Evanston, IL, (2014).
83. Raup, D. M. The future of analytical paleobiology. *Short Courses in Paleontology*, 207–216, https://doi.org/10.1017/S2475263000002208 (1991b).

Acknowledgements

We thank curators and collection managers in those institutions listed in Supplementary Materials Section 3 ('Alabama Marine Vertebrates') for access to fossil specimens under their care. V. Fischer and B. Kear provided technical suggestions on this manuscript. Comments from R.J. Zakrzewski, P.A. Aharon, and J.A. Miyamae helped improved the earlier version of the manuscript. C. Scotese kindly provides permission to use and modify maps for Fig. 1 and Supplementary Fig. S4. Criticisms from anonymous reviewers helped improve this manuscript greatly.

Author contributions

T.I. designed this research and examine those museum specimens. T.I. and Y.L. performed fieldwork and wrote this manuscript. T.I. and B.Z. conducted statistical analyses (including rarefaction by B.Z.). Y.L. and T.I. conducted the SQS analysis using R.

Competing interests

The authors declare no competing interests.

Additional information

Supplementary information is available for this paper at https://doi.org/10.1038/s41598-020-61089-w.

Correspondence and requests for materials should be addressed to T.I.

Reprints and permissions information is available at www.nature.com/reprints.

Publisher's note Springer Nature remains neutral with regard to jurisdictional claims in published maps and institutional affiliations.

Supplementary Materials for

Two-step extinction of Late Cretaceous marine vertebrates in northern Gulf of Mexico prolonged biodiversity loss prior to the Chicxulub impact

By

Takehito Ikejiri, YueHan Lu, and Bo Zhang

This PDF format includes:

1. Geologic Setting

An overview of the geologic setting is available in the main text (Methods and Material) and several references[1–4].

Table S1. Key lithological features of Upper Cretaceous geologic units in Alabama. General features of those units are listed in the main text (Table 1).

Stratigraphic units	Geologic units	Key lithology [1]
Unit 5	Prairie Bluff Chalk Fm	Bluish-gray firm sandy, fossiliferous chalk
	Providence Sandstone Fm	Cross-bedded fine to coarse sand and white, dark-gray, and pale-red-purple mottled clay (upper part); dark gray laminated to thin-bedded silty clay and very fine- to fine-grained sand that is abundantly micaceous and carbonate (lower parts)
Unit 4	Ripley Fm	Light gray to pale olive massive bioturbated micaceous glauconitic fine sand, sandy calcareous clay, thin indurated fossiliferous sandstone (upper part); calcareous sandstone, sandy chalk and coarse cross-bedded sand with occasional thin limestone layers (lower part)
Unit 3	Demopolis Chalk Fm	Light gray to medium light gray fossiliferous chalk; thin marl beds (lower part).
	Bluffport Marl Mbr*	Massive chalky very dark marl, very clayey chalk, calcareous clay
	Cusseta Sand Mbr**	Sandy chalk and coarse cross-bedded sand with occasional thin limestone and fine gravel layers
	Arcola Limestone Mbr***	With 2 to 4 beds of light gray impure dens brittle fossiliferous limestone with softer marl inbedded
Unit 2	Mooreville Chalk Fm	Yellowish-gray to dark bluish-gray clayey compact fossiliferous chalk and chalky marl
	Blufftown Fm	Mainly glauconitic calcareous fine sand; micaceous clay and marl, fossiliferous clay, gray calcareous fossiliferous sandstone, and calcareous clay and silt (locally variable)
Unit 1	Eutaw Fm	Light greenish gray fine to medium-grained well-sorted micaceous cross-bedded sand, fossiliferous and glauconitic in part, containing greenish-gray micaceous silty clay and medium gray-to-dark gray carbonaceous clay

[1] Based on ref. 1.
*A part of the Demopolis Chalk Fm.
**A part of the Reply Fm.
***A part of the Mooreville Chalk Fm.

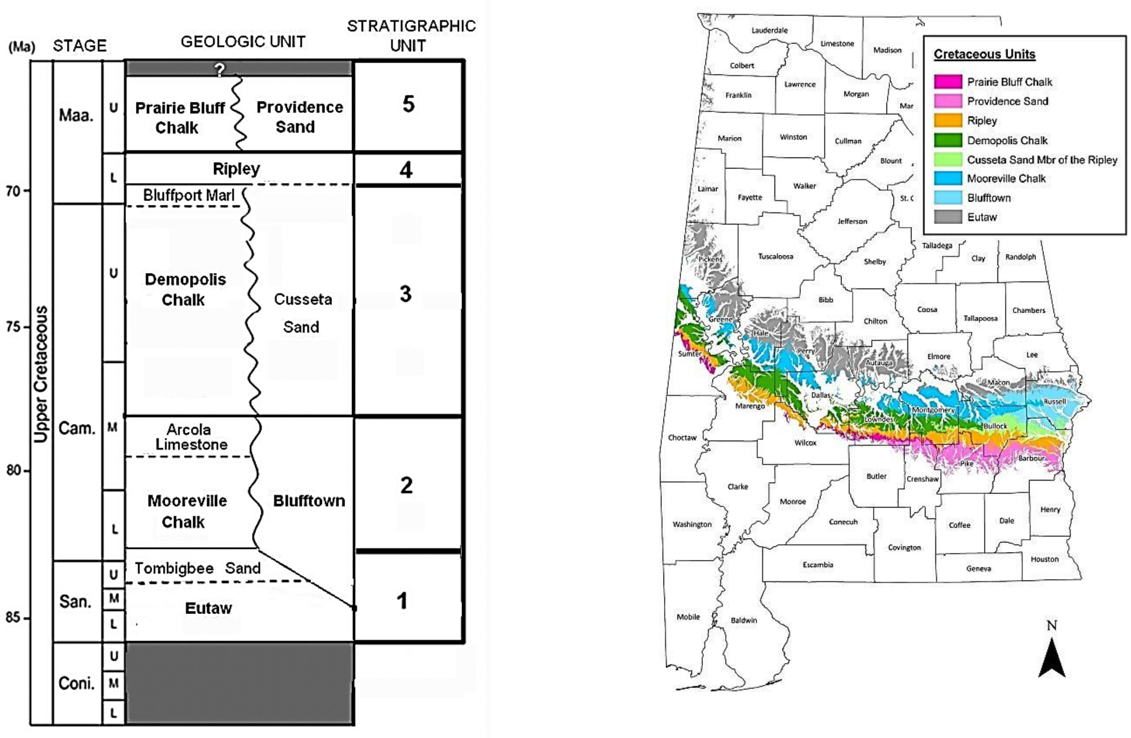


Figure S1. Late Cretaceous stratigraphy (left) and geologic map (right) in Alabama (modified from ref. 4).

Figure S2. Moscow Landing K–Pg boundary site in Sumter County, western Alabama. **Left:** the Upper-most Cretaceous Prairie Bluff Chalk (Kpb) and the lower-most Paleocene Clayton Formation (Tcl) are shown. **Right:** a tooth of marine reptile, *Mosasaurus* sp., in the Clayton Formation. Photos were taken by one of the authors (T.I.) in summer 2015.

2. Analytical Biases and Species Richness Estimation

While examining over 8,275 Cretaceous vertebrate fossil specimens (as some results presented in ref. 4), we are confident that marine vertebrate fossils have been collected thoroughly and systematically in Alabama by the 12 institutions for over 150 years. Marine reptiles and large bony fishes tend to have received special attention by field investigators, as shown in many isolated bones and even incomplete fragmentary specimens housed at the institutions. This collecting emphasis on some specific taxa (e.g., Hybodontiformes, Lamniformes, Ichthyodectiformes, Tselfatiformes, Mosasauridae, Testudinates) yield comprehensive data that reduce the risk of biases for determining extinction patterns.

Of the total of 8,275 specimens, 3,301 specimens have species-level identification with confidence and the information of the stratigraphic unit and fossil locality for data analyses presented in this study (Table 2 in the body text). The largest number of marine vertebrate fossil specimens were collected from Unit 2 while the least number occurred in Unit 4.

Small specimens (e.g., microscopic-sized isolated teeth) are possibly missed to be collected more often than large bones in the field as a case of sampling bias. However, a few specific fossil sites/localities along small rivers or creeks in Alabama can fill this potential gap. For example, a single fossil site along a local creek (the University of Alabama Museums locality number: AGr-43) has been producing a tremendous amount of small isolated teeth and bones that allow identifying, at least, 28 species of rays and sharks from Unit 1 and Unit 2[5]. Such microvertebrate fossil sites reduce the risk of the sampling and/or preservational bias.

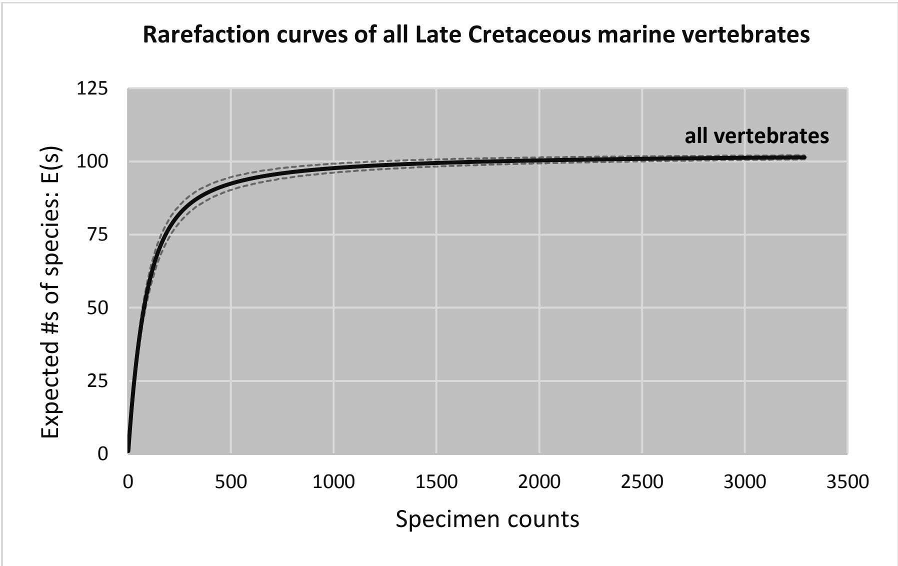
Certain geologic formations or members possibly preserve vertebrate fossils better than others due to variable sedimentological and taphonomic settings. For example, Unit 2 including the Mooreville Chalk and the Blufftown Formation produces the largest number of marine vertebrate species (n=67) and specimens (n=3,978) in Alabama (Table 1) (based on ref. 4). We suggest that this large species count reflects a true diversity pattern, rather than a biased view due to a preservational or collecting bias for the following reasons. First, there is no considerably large difference in the amount of rock volume or surface areas among the Late Cretaceous units (Table 1). An exact rock volume of each geologic unit is physically difficult to measure, but a surface area (in Km^2) and a range of thickness (in meters) allow estimating their relative sizes for quantitative comparisons. The Eutaw Formation in Unit 1 likely shows the largest rock volume, but nearly all vertebrate fossils (943 specimens) concentrate in the upper member (the Tombigbee Sand). The Prairie Bluff Chalk in Unit 5 exhibits considerably low rock volume, but a relatively large specimen number (n = 203) should provide a reasonable data size for determining the fossil abundance relative to other units.

Lithological and sedimentological features are overall consistent throughout Unit 2 to Unit 5, exhibiting mainly light-grayish calcareous chalky layers (Table S1)[1]. The only exceptional case is the Providence Sand (Unit 5), which is characterized by loose sediments (sand and clay) and distributed only in eastern Alabama to western Georgia. The formation has produced only one species and three specimens in total. The Ripley Formation (Unit 4) that is characterized by mostly calcareous sandy chalk has produced a significantly low number of vertebrate species count (n=19 spp.; 95% CI) and a relatively small specimen number (n=139), but invertebrate fossils (especially mollusks) are abundant and often well-preserved (personal observation). Mancini et al. (ref. 3) suggests a series of regression events occurred near the current location of Alabama during the early Maastrichtian. However, no considerably significant changes associated with any drastic environmental changes have been known during the time of Unit 4.

Extinction and diversity patterns are varied among subgroups of vertebrates through the time. Although bony fishes and marine reptiles have the largest degree of occurrence and extinctions in Unit 2, cartilaginous fishes show the biggest decline pattern in Unit 1 (Figs. 2 and 3 in the main text). Moreover, some smaller taxonomic groups show different timings of diversity and extinction peaks through the units (Table 2 in the main text). These variable extinction pathways across various taxonomic groups also indicate that our data represent natural phenomena of the extinction process, instead of biased views. In other words, only if a strong preservational bias is involved, the same or very similar extinction pattern would be expected to be observed across different groups. To sum, a series of circumstantial evidence indicates that our dataset is not strongly biased by sampling and fossil preservation artifacts.

Sampling variation among (1) counties, (2) fossil localities, (3) the surface area of each geologic unit, (4) maximum and (5) median of each unit, and (6) a duration (my) of each unit was investigated by a correlation test (Table 2 in the main text). Although Spearman's rho correlation test tends to be more commonly used for this kind of analysis (e.g., refs. 6 and 7), we used Kendall's tau due expecting a non-linear relation. Because of a small number of data entry (i.e., from the five-time units), the result may not be robust for further interpretation, but it may be a mere reference for an overview of sampling variations. Among the six parameters, the surface area shows the best nature of correlation.

Rarefaction—Expected species counts are calculated based on rarefaction for specimen numbers (Supplementary Fig. S3). In our dataset, a total of 8,275 specimens were collected, and we could identify at the species level for 3,301 of them. The rarefaction curve indicates our data size (i.e., 90 species in total) is reasonable for investigating a diversity analysis. The 3,301 specimens included 1,186 for chondrichthyans (38 species), 897 for bony fish (24 species), and 1,218 for marine reptiles 28 species). The rarefaction curves suggest that chondrichthyans exhibit the best reliable data set and bony fish tends to represent the weakest record.



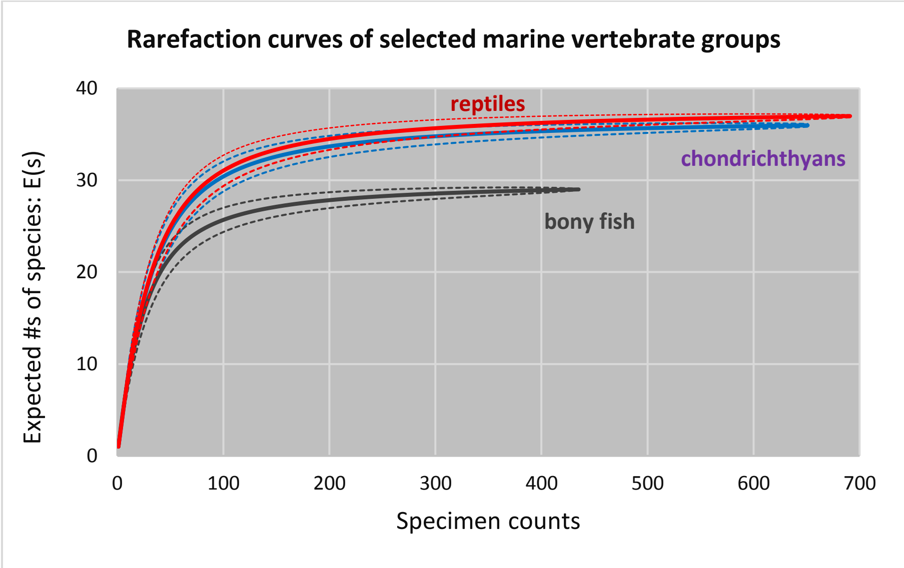


Figure S3. Sample-based rarefaction curves based on the raw data of Cretaceous marine vertebrates. **Top:** all marine vertebrates; **bottom:** cartilaginous fish, bony fish, and marine reptiles. Dotted lines indicate 95% CIs.

Subsampling analysis—Relative fossil richness was estimated by the Shareholder Quorum Subsampling; the quorum, μ, was set at 0.8, 0.4, and 0.2 for comparisons, and a total of 1000 subsampling trials were run for each dataset (using the R code provided by ref. 8). We compared three subgroups of sample-level diversity with all vertebrates through the five geologic units. The result (Figure 2 in the main text; Supplementary Table S2) shows that the highest diversity in Unit 2.

Table S2. The results of the SQS of Cretaceous marine vertebrates. Data with and without singletons are analyzed separately for all vertebrates and the three sub-groups.

All vertebrates

Quorum	**0.8**	**0.6**	**0.4**	**0.2**
Unit 1	26.1	13.6	7.2	2.9
Unit 2	24.6	15.6	9.3	4.2
Unit 3	15.0	9.1	4.9	2
Unit 4	--	7.7	4.7	2
Unit 5	8.3	5.5	3.1	1.3

Cartilaginous fish

Quorum	**0.8**	**0.6**	**0.4**	**0.2**
Unit 1	12.2	6.7	3.7	1.4
Unit 2	8.8	5.6	3.3	1.5
Unit 3	3.6	2	1.2	0.9
Unit 4	5.9	3.9	2.3	0.8
Unit 5	5.3	3.1	1.8	1

Bony fish

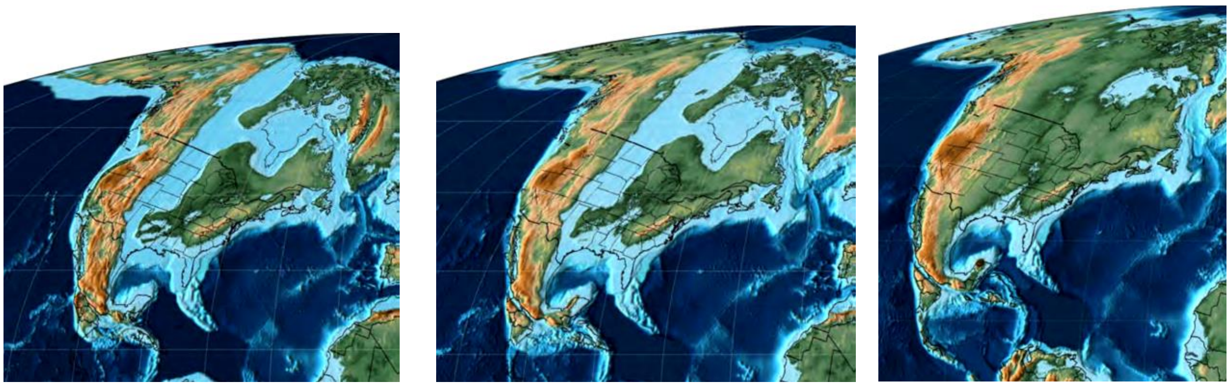
Quarum	**0.8**	**0.6**	**0.4**	**0.2**
Unit 1	9.6	4.9	2.6	1.2
Unit 2	7.8	4.9	2.7	1.2
Unit 3	--	3.9	2.3	1
Unit 4	--	1.6	1	0.4
Unit 5	1.5	1.5	0.5	0.5

Marine reptiles

Quarum	**0.8**	**0.6**	**0.4**	**0.2**
Unit 1	6.9	3.3	1.2	1.1
Unit 2	6.6	3.9	2.2	0.8
Unit 3	--	3.5	2	0.9
Unit 4	--	1.7	1.3	0.6
Unit 5	1.0	1	1	0.4

3. Paleogeography

The current location of Alabama was placed largely in offshore environments along the coastline of the Appalachian landmass through the Late Cretaceous (Supplementary Fig. S4). Alabama was located near the eastern margin of the Mississippian Embayment during the time. The coastline of Alabama had shifted toward south through the Late Cretaceous due to a series of regression events[9]. During the Late Cretaceous, the Western Interior Seaway started to disappear. Our study area represents the northeastern Gulf of Mexico, which is located about 500 km from the Chicxulub impact site as seen in the main text (Fig. 1).



80.3 Ma (Early Campanian) 73.8 Ma (Late Campanian) 66 Ma (end-Maastrichtian)

Figure S4. Paleogeographic maps of North America in Late Cretaceous. **Left.** 80.3 Ma (Early Campanian); **B.** 73.8 Ma (Late Campanian); **C**. 66.0 Ma (Maastrichtian). The position of the paleoshoreline had extended further south in Alabama through the time. Maps modified from Charles Scotese (ref. 10).

4. Alabama Marine Vertebrates

A summary of Late Cretaceous marine vertebrate fossil specimens from Alabama can be found in Ikejiri et al. (ref. 4). Semiaquatic and terrestrial taxa, such as crocodilians, pterosaurs, non-avian dinosaurs, and seabirds were not included in this study. All specimens belong to 12 institutions in the U.S. and U.K., and they are listed as the followings: **AMNH**, American Museum of Natural History, New York, NY, USA; **ANSP**, Academy of Natural Sciences of Philadelphia, PA, USA; **ALMNH**, Alabama Museum of Natural History, University of Alabama, Tuscaloosa, AL, USA; **AUMP**, Auburn University Museum of Paleontology, Auburn, AL, USA; **CCK**, Cretaceous research collections at Columbus State University, Columbus, GA, USA; **CMC**, Cincinnati Museum Center, Cincinnati, OH, USA; **FHSM,** Fort Hays State University Sternberg Museum of Natural History, hays, KS, USA; **FMNH**, Field Museum of Natural History, Chicago, IL, USA; **GSA**, Geological Survey of Alabama, Tuscaloosa, AL (vertebrate fossil collection currently housed at UAM) , USA; **LACM**, Natural History Museum of Los Angeles County Museum, Los Angeles, CA, USA; **MMNS**, Mississippi Museum of Natural Science, Jackson, MS, USA; **MSC**, McWane Science Center, Birmingham, AL, USA; **NHMUK**, Natural History Museum in London, United Kingdom; **NJSM**, New Jersey state Museum, Trenton, NJ, USA; **RMM**, Red Mountain Museum, Birmingham, AL (fossil collection currently housed at MSC) , USA; **UWA**, University of West Alabama, Livingston, AL, USA; **UPI**, Museum of Evolution, Uppsala University, Uppsala, Sweden; **USNM**, United States National Museum, Washington D.C., USA; **YPM**, Yale Peabody Museum, New Haven, CT, USA.

Table S3. Taxonomic list of Late Cretaceous marine vertebrates from Alabama with stratigraphic occurrences. Geologic units (formations and members) for the five stratigraphic units (Unit 1 to 5) are given in the main text (Table 1) and Supplementary Figure S1. Abbreviations for higher taxa: **A**: Actinopterygii (ray-finned fish); **C**: Chondrichthyes; **R**: reptiles (Sauropsida); **S**: Sarcopterygii (lobe-finned fish).

Higher taxa	**Genus**	**Species**	**Stratigraphic occurrences in AL***	**Habitats****	**K–Pg survived in global scale****
Heterodontiformes (C)	*Heterodontus*(?)	sp.	(0)1	nektonic carnivore	Yes (genus)
Hybodontiformes (C)	*Meristodonoides* (cf. *Hybodus*)	sp.	(0) 2	nektonic carnivore	No
Hybodontiformes (C)	*Lissodus*	sp.	(0)- 2	nektonic carnivore	No
Hybodontiformes (C)	*Lonchidion*	sp.	(0) 2	nektonic carnivore	No
Pachycormiformes (A)	*Belonostomus*	sp.	(0),1	nektonic carnivore	No
Chimaeriformes (C)	*Edaphodon*	*mirificus*	(0),2	nektobenthic carnivore	Yes (genus)
Lamniformes (C)	*Paranomotodon*	*angustidens*(?)	(0),2	nektonic carnivore	No
Lamniformes (C)	*Scapanorhynchus*	*rapax*	(0) 2	nektonic carnivore	No
Myliobatiformes (C)	*Rhombodus*	*binkhorsti*	(0)2	nektonic carnivore	No (yes for genus)
Rajiformes (C)	*Dasyatis*	sp.	(0)-2	nektonic carnivore	Yes (genus)
Sclerorhynchiformes (C)	*Sclerorhynchus*	sp.	(0)-2	nektonic carnivore	No
Aulopiformes (A)	*Cimolichthys*	*nepaholica*	(0)-2	nektonic carnivore	No
Crossognathiformes (A)	*Pachyrhizodus*	*caninus*	(0)-2	nektonic carnivore	Yes(?)
Ichthyodectiformes (A)	*Ichthyodectes*	*ctenodon*	(0)-2	nektonic carnivore	No
Ichthyodectiformes (A)	*Saurocephalus*	sp.	(0)-2	nektonic carnivore	Yes
Mosasauridae (R)	*Prognathodon*	sp.	(0)-2	aquatic carnivore	No
Mosasauridae (R)	*Tylosaurus*	*nepaeolicus*(?)	(0)-2	aquatic carnivore	No
Hybodontiformes (C)	*Ptychodus*	*rugosus*	**1**	nektonic carnivore	No
Hybodontiformes (C)	*Ptychodus*	*whipplei*	**1**	nektonic carnivore	No
Lamniformes (C)	*Cretodus*	*semplicatus*	**1**	nektonic carnivore	No
Orectolobiformes (C)	*Cantioscyllium*	sp.	**1**	nektonic carnivore	No
Orectolobiformes (C)	*Chiloscyllium*	*greeni*	**1**	nektonic carnivore	Yes (genus)
Rajiformes (C)	*Pseudohypoliphus*	*mcnultyi*	**1**	nektobenthic carnivore	No(?)
Rajiformes (C)	*Ptychotrygon*	*triangularis*	**1**	nektobenthic carnivore	No
Sclerorhynchiformes (C)	*Borodinopristis*	*schwimmeri*	**1**	nektobenthic carnivore	No
Squatiniformes (C)	*Squatina*	*hassei*	**1**	nektobenthic carnivore	No
Beryciformes (A)	*Hoplopteryx*	sp.	**2**	nektonic carnivore?	No(?)
Tselfatiformes (A)	*Moorevillia*	*hardi*	**2**	nektonic carnivore?	No
Tselfatiformes (A)	*Palelops*	*eutawnesis*	**2**	nektonic carnivore?	No
Pachycormiformes (A)	*Bonnerichthys*	*gladius*	**2**	nektonic carnivore (or planktivore?)	No
Mosasauridae (R)	*Clidastes*	*liodontus* (cf. *C. moorevillensis*)	**2**	aquatic carnivore	No

Plesiosauria (R)	polycotylid	species indet.	**2**	aquatic carnivore	No
Testudines (R)	*Calcarichelys*	*gemma*	**2**	aquatic omnivore	No
Testudines (R)	*Chelosphargis*	*advena*	**2**	aquatic omnivore	No
Testudines (R)	*Corsochelys*	*haliniches*	**2**	aquatic omnivore	No
Testudines (R)	*Ctenochelys*	*tenuitesta*	**2**	aquatic omnivore	No
Testudines (R)	*Lophochelys*	*venatrix*	**2**	aquatic omnivore	No? (the genus survived in the Danian?)
Crossognathiformes (A)	*Pachyrhizodus*	*minimus*	1(?),2	nektonic carnivore	Yes (genus?)
Coelacanthiformes (S)	*Megalocoelacanthus*	*dobiei*	1(?),2	nektobenthic carnivore	No
Lamniformes (C)	*Scapanorhynchus*	*raphiodon*	1,2	nektonic carnivore	No(?)
Lamniformes (C)	*Squalicorax*	*falcatus*	1,2	nektonic carnivore	No
Myliobatiformes (C)	*Brachyrhizodus*	*wichitaensis*	1,2	nektobenthic carnivore(?)	No
Chimaeriformes (C)	*Edaphodon*	*barberi*	1,2	nektobenthic carnivore	Yes (genus)
Hybodontiformes (C)	*Ptychodus*	*polygurus*	1,2	nektonic carnivore	No
Albuliformes (A)	*Albula*	*dunklei*	1,2	nektobenthic carnivore	No
Pachycormiformes (A)	*Protosphyraena*	*nitida*	1,2	nektonic carnivore	No
Pycnodontiformes (A)	*Hadrodus*	*priscus*	1,2	nektonic durophage-carnivore	No
Pycnodontiformes (A)	*Phacodus*	*puncatus*	1,2	nektonic durophageo & carnivore	No(?)
Tselfatiformes (A)	*Bananogmius*	*crieleyi*	1,2	nektonic carnivore	Yes
Mosasauridae (R)	*Eonatator*	*sternbergi*	1,2	aquatic carnivore	No
Mosasauridae (R)	*Platecarpus*	*tympaniticus*	1,2	aquatic carnivore	No
Mosasauridae (R)	*Selmasaurus*	*russelli*	1,2	aquatic carnivore	No
Plesiosauria (R)	elasmosaurid	species indet.	1,2	aquatic carnivore	No
Testudines (R)	*Thinochelys*	*lapisossea*	1,2	aquatic omnivore	No
Mosasauridae (R)	*Mosasaurus*	*missouriensis*(?)	**3**	aquatic carnivore	No
Mosasauridae (R)	*Mosasaurus*	*conodon*	**3**	aquatic carnivore	No
Mosasauridae (R)	*Platecarpus*	cf. *somenensis*	**3**	aquatic carnivore	No
Hybodontiformes (C)	*Ptychodus*	*mortoni*	1,2,3	nektonic carnivore	No
Aulopiformes (A)	*Enchodus*	*petrosus*	1,2,3	nektonic carnivore	Yes
Aulopiformes (A)	*Stratodus*	*apicalis*	1,2,3	nektonic carnivore	No
Mosasauridae (R)	*Tylosaurus*	*proriger*	1,2,3	aquatic carnivore	No
Testudines (R)	*Chedighaii*	*baeberi*	1,2,3	aquatic omnivore	yes (sister taxon: *Bothremys*)
Mosasauridae (R)	*Clidastes*	*propython*	1(?),2,3	aquatic carnivore	No
Aulopiformes (A)	*Enchodus*	*gladiolus*	2,3	nektonic carnivore	Yes
Ichthyodectiformes	*Saurodon*	*leanus*	2,3	nektonic carnivore	No

Mosasauridae (R)	*Globidens*	*alabamaensis*	2,3	aquatic carnivore	No
Testudines (R)	*Prionochelys*	*matutina*	2,3	aquatic omnivore	No
Testudines (R)	*Toxochelys*	*moorevillensis*	2,3	aquatic omnivore	No
Lamniformes (C)	*Pseudocorax*	*laevis*	1,2,4	nektonic carnivore	No
Ichthyodectiformes (A)	*Xiphactinus*	*audax*	1,2,4	nektonic carnivore	No
Aulopiformes (A)	*Enchodus*	*ferox*	2,3,4	nektonic carnivore	Yes
Testudines (R)	*Ctenochelys*	*acris*	2,4	aquatic omnivore	No
Myliobatiformes (C)	*Pseudohypolophus*	*mcnultyi*	**5**	nektobenthic carnivore	No(?)
Orectolobiformes (C)	*Ginglymostoma*	sp.	**5**	nektobenthic carnivore	Yes (genus)
Rajiformes (C)	*Sclerorhynchus*	sp.	**5**	nektonic carnivore	No
Aulopiformes (A)	*Enchodus*	sp.	5	nektonic carnivore	No
Lamniformes (C)	*Squalicorax*	*kaupi*	1,2,3,5	nektonic carnivore	No
Lamniformes (C)	*Cretoxyrhina*	*mantelli*	1,2,3,5	nektonic carnivore	No
Sclerorhynchiformes? (C)	*Ischyrhiza*	*mira*	1,2,3,5	nektonic carnivore	Yes
Mosasauridae (R)	*Plioplatecarpus*	sp.	1,2,3,5	aquatic carnivore	No
Lamniformes (C)	*Cretalamna*	*appendiculata*	1,2,4,5	nektonic carnivore	Yes
Pycnodontiformes (A)	*Anomoeodus*	*phaseolus*	1,2,4,5	nektonic durophage-carnivore	No
Lamniformes (C)	*Scapanorhynchus*	*texanus*	1,2,3,4,5	nektonic carnivore	No
Lamniformes (C)	*Serratolamna*	*serrata*	1,2,5	nektonic carnivore	No
Lamniformes (C)	*Carcharias*(?)	sp.	1(?),5	nektonic carnivore	Yes (genus)
Lamniformes (C)	*Squalicorax*	*pristodontus*	2,3,4,5	nektonic carnivore	No
Testudines (R)	*Protostega*	*gigas*	2,3,5(?)	aquatic omnivore	No
Mosasauridae (R)	*Mosasaurus*	*maximus*	3,4,5	aquatic carnivore	No

*Data updated from Ikejiri et al. (ref. 4). Bold numbers indicate singleton taxa. The occurrence of Unit 0 is based on data from the Western Interior Seaway and other parts of the Gulf of Mexico (see the additional explanation in Methods).
**Data from the Paleobiology Database[11].

Table S4. Marine vertebrate taxa from the Paleocene identified from Alabama. The detail is currently understudied by one of the authors (T.I.).

Geologic units	Sharks	Bony fish	Reptile
Impact deposits:	*Squalicorax pristodontus*(?);	*Enchodus* sp.	*Mosasaurus maximus*
Clayton Fm:	*Cretalamna* sp.; *Sphenodus* sp.; *Striatolamina* sp.	*Enchodus*(?).	

Table S5. Data on species counts and origination and extinction rates used for Figure 3 and Figure 4 in the main text. Temporarily disappeared taxa (Lazarus taxa) were included. An asterisk mark indicates a significantly high extinction value (based on the upper 95% CI).

All Vertebrates (with singletons)

Stratigraphic unit	species count Occurred	Originate	Extinct	Standing diversity	Percentage Originate	Extinct	Error bar (lower) Extinct	(upper) Extinct
Santonian (Unit 0)	12.0	--	--	--	--	--		
Unit 1	60*	43*	9	44.0	71.67%*	15.00%	30.89%	12.22%
Unit 2	68*	20	40*	51.0	29.41%	58.82%	80.60%	49.29%
Unit 3	29	4	13	24.0	13.79%	44.83%	51.00%	26.89%
Unit 4	17	0	3	14.5	0.00%	17.65%	27.22%	10.67%
Unit 5	18	4	15	13.5	22.22%	83.33%*	96.24%	61.66%
Paleocene	4	3?	0?	1.5	--	--		
Sum (Unit 1-5)	192	71	80					
MEAN	38.4	14.2	16		27.42%	43.93%		
SD	24.0	17.8	14.2		27.05%	28.74%		
95% CI	21.0	15.6	12.4		23.71%	25.19%		
Upper	59.4	29.8	28.4		51.13%	69.11%		
Lower	17.4	-1.4	3.6		3.71%	18.74%		

All Vertebrates (without singletons)

Stratigraphic unit	species count Occurred	Originate	Extinct	Standing diversity	Percentage Originate	Extinct	Error bar (lower) Extinct	(upper) Extinct
Santonian (Unit 0)	12	--	--	--	--	--	--	--
Unit 1	45*	29*	3	17.5	64.44%*	6.67%	22.23%	7.65%
Unit 2	51*	9	25*	17.5	17.65%	49.02%	77.23%	46.66%
Unit 3	27	1	9	5.0	3.70%	33.33%	45.17%	22.72%
Unit 4	17	0*	5	1.5	0.00%	29.41%	38.10%	17.79%
Unit 5	15	0	9	5.5	0.00%	60.00%*	79.48%	48.41%
Paleocene (Unit 6)	4?	3?	0?	2	--	--		
Sum (Unit 1-5)	155	39	51					
MEAN	31	7.8	10.2		17.16%	35.69%		
SD	16.3	12.4	8.7		27.41%	20.35%		
95% CI	14.3	10.9	7.6		24.03%	17.83%		
Upper	45.3	18.7	17.8		41.19%	53.52%		
Lower	16.7	-3.1	2.6		-6.87%	17.85%		

Cartilaginous fishes (with singletons)

Stratigraphic Unit	Species count (#s)			Percentage		Error bar (lower)	Error bar (upper)
	Occurred	**Originate**	**Extinct**	**Origination**	**Extinction**	**Extinction**	**Extinction**
Unit 1	33*	23*	11	69.70%*	33.33%	46.34%	23.55%
Unit 2	22	1	13*	4.55%	59.09%	76.11%	45.79%
Unit 3	10	0	1	0.00%	10.00%	30.88%	12.22%
Unit 4	8	0	1	0.00%	12.50%	20.96%	6.92%
Unit 5	10	3	9	30.00%	90.00%*	110.63%	72.37%
Sum	83	27	35				
MEAN	16.6	5.4	7	20.85%	40.98%		
SD	10.7	9.9	5.7	30.02%	33.77%		
95% CI	9.4	8.7	5.0	26.31%	29.60%		
Upper	26.0	14.1	12.0	47.16%	70.58%		
Lower	7.2	-3.3	2.0	-5.47%	11.39%		

Cartilaginous fishes (without singletons)

Stratigraphic Unit	Species count (#s)			Percentage		Error bar (lower)	Error bar (upper)
	Occurred	**Originate**	**Extinct**	**Origination**	**Extinction**	**Extinction**	**Extinction**
Unit 1	20*	8*	1	40.00%*	5.00%	29.67%	12.22%
Unit 2	20*	1	10*	5.00%	50.00%	90.67%	57.22%
Unit 3	10	0	1	0.00%	10.00%	4.80%	17.08%
Unit 4	8	0	1	0.00%	12.50%	18.39%	4.80%
Unit 5	8	0	5	0.00%	62.50%*	83.97%	51.92%
Sum	66	9	18				
MEAN	13.2	1.8	3.6	9.00%	28.00%		
SD	6.3	3.5	4.0	17.46%	26.30%		
95% CI	5.5	3.1	3.5	15.31%	23.06%		
Upper	18.7	4.9	7.1	24.31%	51.06%		
Lower	7.7	-1.3	0.1	-6.31%	4.94%		

Bony fishes (with singletons)

Stratigraphic Unit	Species count (#s)			Percentage		Error bar (lower)	(upper)
	Occurred	Originate	Extinct	Origination	Extinction	Extinction	Extinction
Unit 1	17	11*	1	64.71%*	5.88%	11.67%	2.20%
Unit 2	22*	6	15*	27.27%	68.18%*	86.21%	53.69%
Unit 3	7	0	2	0.00%	28.57%	23.49%	8.40%
Unit 4	5	0	1	0.00%	20.00%	30.88%	12.22%
Unit 5	5	1	2	20.00%	40.00%	54.47%	28.58%
Sum	56	18	21				
MEAN	11.2	3.6	4.2	22.40%	32.53%		
SD	7.8	4.8	6.1	26.57%	23.50%		
95% CI	6.9	4.2	5.3	23.28%	20.60%		
Upper	18.1	7.8	9.5	45.68%	53.13%		
Lower	4.3	-0.6	-1.1	-0.89%	11.93%		

Bony fishes (without singletons)

Stratigraphic Unit	Species count (#s)			Percentage		Error bar (lower)	(upper)
	Occurred	Originate	Extinct	Origination	Extinction	Extinction	Extinction
Unit 1	15*	12*	1	80.00%*	6.67%	17.08%	4.80%
Unit 2	17*	3	10*	17.65%	58.82%*	77.23%	46.66%
Unit 3	7	0	3	0.00%	42.86%	40.47%	19.42%
Unit 4	5	0	2	0.00%	40.00%	54.47%	28.58%
Unit 5	4	0	1	0.00%	25.00%	36.90%	16.18%
Sum	48	15	17				
MEAN	9.6	3	3.4	19.53%	34.67%		
SD	6.0	5.2	3.8	34.66%	19.73%		
95% CI	5.2	4.6	3.3	30.38%	17.29%		
Upper	14.8	7.6	6.7	49.91%	51.96%		
Lower	4.4	-1.6	0.1	-10.85%	17.38%		

Marine reptiles (with singletons)

Stratigraphic Unit	Species count (#s)			Percentage		Error bar (lower)	Error bar (upper)
	Occurred	Originate	Extinct	Origination	Extinction	Extinction	Extinction
Unit 1	10	9	0	90.00%*	0.00%	3.69%	0.00%
Unit 2	24*	13*	15*	54.17%	62.50%	79.48%	48.41%
Unit 3	13	4	9	30.77%	69.23%	87.32%	54.57%
Unit 4	4	0	1	0.00%	25.00%	36.90%	16.18%
Unit 5	3	0	3	0.00%	100.00%*	121.63%	81.36%
Sum	54	26	28				
MEAN	10.8	5.2	5.6	34.99%	51.35%		
SD	8.5	5.7	6.3	38.28%	39.19%		
95% CI	7.4	5.0	5.5	33.55%	34.35%		
Upper	18.2	10.2	11.1	68.54%	85.69%		
Lower	3.4	0.2	0.1	1.44%	17.00%		

Marine reptiles (without singletons)

Stratigraphic Unit	Species count (#s)			Percentage		Error bar lower	Error bar upper
	Occurred	Originate	Extinct	Origination	Extinction	extinction	extinction
Unit 1	10	9*	1	90.00%*	10.00%	14.42%	3.45%
Unit 2	14*	5	5	35.71%	35.71%	55.62%	30.27%
Unit 3	10	1	6*	10.00%	60.00%	77.23%	45.79%
Unit 4	4	0	2	0.00%	50.00%	65.92%	37.11%
Unit 5	3	0	3	0.00%	100.00%*	121.63%	81.36%
Sum	41	15	17				
MEAN	8.2	3	3.4	27.14%	51.14%		
SD	4.6	3.9	2.1	38.05%	33.16%		
95% CI	4.0	3.5	1.8	33.35%	29.06%		
Upper	12.2	6.5	5.2	60.50%	80.21%		
Lower	4.2	-0.5	1.6	-6.21%	22.08%		

Table S6. Extinction rates of all marine vertebrates based on the data excluding singleton taxa. The data of *p* and *q* are used in Figure 5.

A. All vertebrates

Quantity	symbol (1)	Unit 1	Unit 2	Unit 3	Unit 4	Unit 5
Duration in million years (m.y.)	k	3 m.y.	5 m.y.	8 m.y.	2 m.y.	4 m.y.
Singleton taxa		15	17	3	0	3
# of taxa crossing both lower and upper boundaries	N bt	9	18	16	14	4
Originate # (w/o singletons)	N b	6	9	1	0	0
Extinct # (w/o singletons)	N t	6	26	9	3	11
Standing diversity (w/o singletons)		6.0	17.5	5.0	1.5	5.5
Proportional origination	PO	0.67	0.50	0.06	0.00	0.00
Proportional extinction	PE	0.67	1.44	0.56	0.21	2.75
Proportional origination rate per-m.y.	PO m.y.	0.22	0.10	0.01	0.00	0.00
Proportional extinction rate per-m.y.	PE m.y.	0.22	0.29	0.07	0.11	0.69
Per-capita origination rate (per Lmy)	*p*	-0.14	-0.14	-0.35	--	--
Per-capita extinction rate (per Lmy)	*q*	-0.14	0.07	-0.07	-0.77	0.25

(1) Equivalences of symbols are from refs. 12 and 13.

B. Cartilaginous fish

Unit	symbol (1)	Unit 1	Unit 2	Unit 3	Unit 4	Unit 5
Singleton taxa		13	2	0	0	2
# of taxa crossing both lower and upper boundaries	N bt	4	9	8	7	1
Originate # (w/o singletons)	N b	1	10	1	1	5
Extinct # (w/o singletons)	N t	1	10	1	1	5
Standing diversity (w/o singletons)	N st	4.5	5.5	0.5	0.5	2.5
Proportional origination	PO	2.00	0.11	0.00	0.00	0.00
Proportional extinction	PE	0.25	1.11	0.13	0.14	5.00
Proportional origination rate per-m.y.	PO m.y.	0.67	0.02	0.00	0.00	0.00
Proportional extinction rate per-m.y.	PE m.y.	0.08	0.22	0.02	0.07	1.25
Per-capita origination rate (per Lmy)	*p*	0.23	-0.44	--	--	--
Per-capita extinction rate (per Lmy)	*q*	-0.46	0.02	-0.26	-0.97	0.40

(1) Equivalences of symbols are from refs. 12 and 13.

Table S6 (cont.)

C. Bony fish

Unit	symbol (1)	Unit 1	Unit 2	Unit 3	Unit 4	Unit 5
Singleton taxa		5	0	0	1	0
# of taxa crossing both lower and upper boundaries	N bt	14	7	4	3	3
Originate # (w/o singletons)	N b	12	3	0	0	0
Extinct # (w/o singletons)	N t	1	10	3	2	1
Standing diversity (w/o singletons)	N st	6.5	6.5	1.5	1	0.5
Proportional origination	PO	0.86	0.43	0.00	0.00	0.00
Proportional extinction	PE	0.07	1.43	0.75	0.67	0.33
Proportional origination rate per-m.y.	PO m.y.	0.29	0.09	0.00	0.00	0.00
Proportional extinction rate per-m.y.	PE m.y.	0.02	0.29	0.09	0.33	0.08
Per-capita origination rate (per Lmy)	*p*	-0.05	-0.17	--	--	--
Per-capita extinction rate (per Lmy)	*q*	-0.88	0.07	-0.04	-0.20	-0.27

(1) Equivalences of symbols are from refs. 12 and 13.

D. Marine reptiles

Unit	symbol (1)	Unit 1	Unit 2	Unit 3	Unit 4	Unit 5
Singleton taxa		0	10	3	0	0
# of taxa crossing both lower and upper boundaries	N bt	1	3	3	3	0
Originate # (w/o singletons)	N b	9	5	1	0	0
Extinct # (w/o singletons)	N t	1	5	6	2	3
Standing diversity (w/o singletons)	N st	5	5	3.5	1	1.5
Proportional origination	PO	9.00	1.67	0.33	0.00	--
Proportional extinction	PE	1.00	1.67	2.00	0.67	--
Proportional origination rate per-m.y.	PO m.y.	3.00	0.33	0.04	0.00	--
Proportional extinction rate per-m.y.	PE m.y.	0.33	0.33	0.25	0.33	--
Per-capita origination rate (per Lmy)	*p*	0.73	0.10	-0.14	--	--
Per-capita extinction rate (per Lmy)	*q*	0.00	0.10	0.09	-0.20	--

(1) Equivalences of symbols are from refs. 12 and 13.

5. Global Extinction Pattern of Cretaceous Marine Vertebrates

On a worldwide scale, a total of 396 genera of marine vertebrates were recorded from the Cenomanian to Paleocene. Of the 690 total occurrences, the total generic counts show no significant decline (95% CI) through the Maastrichtian–Paleocene boundary (Table S7 and Table S8). Of the three vertebrate groups, a significant level of the decline occurred only in reptiles from the Maastrichtian to the Paleocene, indicating that marine reptiles (esp., mosasaurs and plesiosaurs) faced severe damage. To some degree, this marine vertebrate extinction pattern on the global scale resembles the pattern found in Alabama fauna.

Table S7. The generic-level occurrence of Late Cretaceous and Paleocene marine vertebrates on a global scale. Data were downloaded from the Paleobiology Database[11] (accessed in January 2019). Questionable and possible non-marine taxa were not included. Vertebrate genera used for this analysis are listed in Supplementary Table S8.

	All vertebrates	Cartilaginous fishes	Bony fishes	Reptiles
Cenomanian	108*	44*	39	25
Santonian	133	47	33	53
Campanian	151	82	31	38
Maastrichtian	154	69	29	56
Paleocene	144	64	58	22*
Total occurrence	690	306	190	194
Mean ± SD	138.0±18.6	61.2±15.8	38.0±11.8	38.8±15.6
95% CI (lower limit)	119.4	45.4	26.2	23.2
Total genera count	396	139	124	133
K–Pg victims	102	39	17	46
K–Pg survivors	51	31	11	9
Newly appeared genera in Paleocene	93	33	47	13

*Asterisk symbols indicate significantly low counts based on the 95% CI.

Table S8. A list of marine vertebrate genera from the Late Cretaceous to Paleocene on a global scale. Data are selected from the Paleobiology Database (ref. 11; http://fossilworks.org). A summary of generic counts through the K–Pg boundary can be found in Table S5. Total numbers of species are also listed for each genus from the database, but alpha taxonomy needs to be clarified for some of them. As such, specific names are not listed (available in the database) and analyzed in this study. **Abbreviations for ages: Ce**: Cenomanian; **Sa**: Santonian; **Ca**: Campanian; **Ma**: Maastrichtian; **Pa**: Paleocene. Taxa with an asterisk mark indicate the pre-Unit 1 (i.e., Unit 0: early to mid-Santonian) occurrence, which is used for Lazarus taxon counts (see '0' occurrence in Supplementary Table S3).

(a). Cartilaginous fishes

Chondrichthyes	Genus	#s of species	Age
Chimaeriformes	*Edaphodon**	7	Ce–Pa
Chimaeriformes	*Ischyodus**	4	Ce–Pa
Chimaeriformes	*Elasmodus*	1	Ce–Ma
Heterodontiformes	*Heterodontus**	4	Ce–Pa
Hexanchiformes	*Heptranchias*	1	Pa
Hexanchiformes	*Hexanchus*	4	Sa–Pa
Hexanchiformes	*Notidanodon*	3	Ca–Pa
Hexanchiformes	*Notorhynchus*	1	Pa
Hexanchiformes	*Weltonia*	1	Pa
Hexanchiformes	*Chlamydoselachus*	1	Pa
Hybodontiformes	*Asteracanthus*	1	Ca
Hybodontiformes	*Hybodus**	4	Ce–Ma
Hybodontiformes	*Lissodus(*	2	Sa–Ma
Hybodontiformes	*Lonchidion*	1	Ma
Hybodontiformes	*Polyacrodus*	1	Ce–Ca
Hybodontiformes	*Ptychodus**	8	Ce–Ca
Carchariniformes	*Physogaleus*	1	Pa
Carchariniformes	*Crassescyliorhinus*	1	Ca
Carchariniformes	*Foumtizia*	1	Pa
Carchariniformes	*Premontreia*	1	Pa
Carchariniformes	*Pteroscyllium*	2	Ca–Ma
Carchariniformes	*Abdounia*	3	Pa
Carchariniformes	*Galeorhinus*	5	Ca–Pa
Carchariniformes	*Pachygaleus*	1	Pa
Carchariniformes	*Palaeogaleus*	5	Ca–Pa
Carchariniformes	*Paratriakis*	1	Sa–Ca
Carchariniformes	*Protoscyliorhinus*	1	Ce
Carchariniformes	*Scyliorhinus*	8	Ca–Pa
Carchariniformes	*Squatigaleus*	1	Ca–Ma
Carchariniformes	*Triakis*	1	Pa
Lamniformes	*Pseudocorax*	3	Sa–Ma
Lamniformes	*Squalicorax*	11	Ce–Pa(?)
Lamniformes	*Archaeolamna*	2	Ce–Ca
Lamniformes	*Cardabiodon*	1	Ce
Lamniformes	*Cretalamna*	8	Ca
Lamniformes	*Cretodus*	4	Ce–Ma
Lamniformes	*Cretoxyrhina*	1	Ce–Ca
Lamniformes	*Dallasiella*	1	Ce
Lamniformes	*Plicatolamna*	2	Ce–Ma
Lamniformes	*Serratolamna*	3	Ca–Ma
Lamniformes	*Leptostyrax*	1	Sa
Lamniformes	*Protolamna*	3	Ce–Ca
Lamniformes	*Oxyrhina*	4	Ca–Pa

Lamniformes	*Hypotodus*	2	Ca–Ma
Lamniformes	*Jaekelotodus*	1	Pa
Lamniformes	*Palaeohypotodus*	2	Ma–Pa
Lamniformes	*Carcharodon*	2	Pa
Lamniformes	*Corax*	1	Ca
Lamniformes	*Isurus*	2	Ce–Pa
Lamniformes	*Lamna*	7	Ce–Pa
Lamniformes	*Orthacodus*	1	Pa
Lamniformes	*Anomotodon*	3	Sa–Ma
Lamniformes	*Woellsteinia*	1	Pa
Lamniformes	*Brachycarcharias*	1	Pa
Lamniformes	*Carcharias*	16	Ce–Pa
Lamniformes	*Cenocarcharias*	2	Ce
Lamniformes	*Eostriatolamia*	1	Ce–Ca
Lamniformes	*Odontaspis*	17	Ce–Pa
Lamniformes	*Pseudodontaspis*	3	Ca–Pa
Lamniformes	*Pseudoisurus*	2	Ce
Lamniformes	*Striatolamia*	3	Pa
Lamniformes	*Synodontaspis*	3	Sa–Ma
Lamniformes	*Cretalamna*	2	Ce–Ca
Lamniformes	*Palaeocarcharodon*	1	Pa
Lamniformes	*Scapanorhynchus**	6	Ce–Pa(?)
Lamniformes	*Paranomotodon**	1	Sa–Ma
Selachii	*Mustelus*	1	Pa
Selachii	*Sphyrna*	1	Pa
Myliobatiformes	*Coupatezia*	1	Pa
Myliobatiformes	*Dasyatis**	10	Ma–Pa
Myliobatiformes	*Igdabatis*	2	Ma
Myliobatiformes	*Myliobatis*	1	Pa
Myliobatiformes	*Rhinoptera*	1	Ca–Pa
Myliobatiformes	*Rhombodus*	1	Ca
Myliobatiformes	*Hypolophites*	1	Pa
Myliobatiformes	*Hypolophodon*	1	Pa
Myliobatiformes	*Palaeodasyatis*	1	Pa
Myliobatiformes	*Viperecucullus*	1	Pa
Myliobatiformes	*Aetobatus*	2	Pa
Myliobatiformes	*Igdabatis*	2	Ma
Myliobatiformes	*Myliobatis*	7	Ma–Pa
Myliobatiformes	*Pseudohypolophus*	2	Sa–Ca
Myliobatiformes	*Pucabatis*	1	Ma
Myliobatiformes	*Rhinoptera*	1	Pa
Myliobatiformes	*Rhombodus**	6	Ca–Pa
Myliobatiformes	*Brachyrhizodus*	2	Sa–Ma
Myliobatiformes	*Coupatezia*	2	Ca–Pa
Myliobatiformes	*Texabatis*	1	Ma
Myliobatiformes	*Turoniabatis*	1	Ce
Pristiformes	*Onchopristis*	1	Ce
Pristiformes	*Peyeria*	1	Ce
Pristiformes	*Pristis*	1	Pa
Orectolobiformes	*Ginglymostoma*	3	Pa
Pristiformes	*Cyclobatis*	3	Ce
Pristiformes	*Cederstroemia*	1	Ca
Pristiformes	*Dalpiazia*	1	Ca–Ma
Pristiformes	*Onchopristis*	2	Ce–Ca
Pristiformes	*Pristis*	1	Pa
Pristiformes - Orectolobiformes	*Ginglymostoma*	2	Ca–Ma

Pristiformes - Orectolobiformes	*Cantioscyllium*	3	Ce–Ma
Pristiformes - Orectolobiformes	*Nebrius*	1	Ma–Pa
Pristiformes - Orectolobiformes	*Plicatoscyllium*	4	Ca–Ma
Pristiformes - Orectolobiformes	*Chiloscyllium*	4	Sa–Ma
Pristiformes - Orectolobiformes	*Hemiscyllium*	1	Ca–Ma
Pristiformes - Orectolobiformes	*Almascyllium*	1	Ce–Sa
Pristiophoriformes	*Pristiophorus*	2	Sa–Ma
Squaliformes	*Centrophoroides*	2	Ca
Squaliformes	*Centrophorus*	1	Ca–Pa
Squaliformes	*Centroscymnus*	4	Ca–Ma
Squaliformes	*Dalatias*	1	Pa
Squaliformes	*Eoetmopterus*	1	Ca
Squaliformes	*Megasqualus*	1	Pa
Squaliformes	*Procentrophorus*	1	Ce
Squaliformes	*Protosqualus*	1	Ce–Ma
Squaliformes	*Pseudoechinorhinus*	2	Pa
Squaliformes	*Squaliodalatias*	1	Ce
Squaliformes	*Squalus*	4	Ce–Pa
Synechodontiformes	*Paraorthacodus*	3	Ce–Pa
Synechodontiformes	*Synechodus*	8	Ce–Pa
Rajiformes	*Hypolophus*	1	Ce–Ca
Rajiformes	*Ischyrhiza*	10	Sa–Pa
Rajiformes	*Tethybatis*	1	Ca–Ma
Rajiformes	*Raja*	3	Ce–Ma
Rajiformes	*Erguitaia*	2	Ca–Ma
Rajiformes	*Hamrabatis*	2	Ca–Ma
Rajiformes	*Parapalaeobates*	2	Ca–Ma
Rajiformes	*Paratrygonorrhina*	1	Ca
Rajiformes	*Protoplatyrhina*	1	Ca–Ma
Rajiformes	*Rhinobatos*	1	Ca–Pa
Rajiformes	*Rhinobatos*	14	Ce–Pa
Rajiformes	*Rhombopterygia*	1	Ce
Sclerorhynchiformes	*Ankistrorhynchus*	2	Sa–Ca
Sclerorhynchiformes	*Borodinopristis*	1	Sa–Ca
Sclerorhynchiformes	*Ctenopristis*	2	Ca–Pa
Sclerorhynchiformes	*Ganopristis*	1	Ca–Ma
Sclerorhynchiformes	*Micropristis*	1	Ce
Sclerorhynchiformes	*Ptychotrygon*	10	Ce–Ma
Sclerorhynchiformes	*Schizorhiza*	1	Ca–Ma
Sclerorhynchiformes(?)	*Sclerorhynchus**	3	Sa–Ma

(b). Bony fishes

Actinopterygii	Genus	#s of species	Age
Acipenseriformes	*Acipenser*	3	Ca–Pa
Acipenseriformes	*Propenser*	1	Sa–Pa
Albuliformes	*Albula*	3	Sa–Pa
Albuliformes	*Albulidarum*	1	Pa
Albuliformes	*Anogmius*	1	Sa–Ca
Albuliformes	*Cretalbula*	1	Ce
Albuliformes	*Farinichthys*	1	Pa
Albuliformes	*Lebonichthys*	1	Ce
Albuliformes	*Moorevillia*	1	Sa
Albuliformes	*Pterothrissus*	1	Pa
Albuliformes	*Pteralbula*	1	Pa
Araripichthyidae	*Araripichthys*	1	Sa
Alepisauriformes	*Apateodus*	1	Ce–Ma
Argentiniformes	*Argentina*	2	Pa
Argentiniformes	*Protoargentinolithus*	1	Pa
Argentiniformes	*Protoargentinolithus*	1	Pa
Anguilliformes	*Rhynchoconger*	1	Pa
Anguilliformes	*Rhechias*	1	Pa
Anguilliformes	*Conger*	1	Pa
Anguilliformes	*Urenchelys*	1	Sa
Anguilliformes	*Luenchelys*	1	Ce
Anguilliformes	*Pseudoegertonia*	1	Ca–Pa
Aulopiformes	*Chlorophthalmus*	1	Pa
Aulopiformes?	*Stratodus*	1	Ce–Ma
Aulipiformes	*Cimolichthys*	1	Sa–Ca
Aulipiformes	*Enchodus*	17	Ce–Pa
Aulopiformes?	*Eurypholis*	1	Ce
Aulopiformes?	*Parenchodus*	1	Ce
Aulopiformes	*Serrilepis*	3	Ce
Beryciformes	*Beryx*	1	Ca–Ma
Beryciformes	*Centroberyx*	3	Pa
Beryciformes	*Hoplostethus*	1	Pa
Beryciformes	*Judeoberyx*	1	Ce
Beryciformes	*Paracentrus*	1	Ce
Beryciformes	*Hoplopteryx*	1	Sa–Ca
Beryciformes	*Trachichthyidarum*	1	Pa
Carangiformes	*Carangidarum*	1	Pa
Clupeiformes	*Clupeidarum*	1	Pa
Clupeiformes	*Armigatus*	2	Ce
Crossognathiformes	*Apsopelix*	1	Sa
Dercetidae	*Cylindracanthus*	1	Ca–Pa
Dercetidae	*Dercetis*	1	Ma
Dercetidae	*Rhynchodercetis*	3	Ce
Ellimmichthyiformes	*Rhombichthys*	1	Ce
Ellimmichthyiformes	*Triplomystus*	2	Ce
Ellimmichthyiformes	*Tycheroichthys*	1	Ce
Elopiformes	*Ctenodentelops*	1	Ce
Elopiformes	*Elopopsis*	1	Ce

Elopiformes	*Palelops*	1	Sa–Ca
Elopiformes	*Pachyrhizodus**	4	Ce–Pa(?)
Elopiformes	*Paralbula*	1	Ce–Ma
Elopiformes	*Egertonia*	1	Ca
Elopiformes	*Osmeroides*	1	Sa
Esociformes	*Estesesox*	1	Ca
Gadiformes	*Protocolliolus*	1	Pa
Gadiformes	*Gadomorpholithus*	1	Pa
Gadiformes	*Molva*	1	Pa
Gadiformes	*Coryphaenoides*	1	Pa
Gadiformes	*Hymenocephalus*	1	Pa
Gadiformes	*Palaeogadus*	1	Pa
Gadiformes	*Raniceps*	1	Pa
Gadiformes	*Maorigadus*	1	Pa
Gonorhynchiformes	*Judeichthys*	1	Ce
Gonorhynchiformes	*Ramallichthys*	1	Ce
Ichthyodectiformes	*Ghrisichthys*	1	Sa
Ichthyodectiformes	*Ichthyodectes**	1	Ce -Ca
Ichthyodectiformes	*Xiphactinus**	2	Ce–Ma
Ichthyodectiformes	*Gillicus*	1	Sa–Ca
Ichthyodectiformes	*Saurocephalus*	1	Ce–Ma
Ichthyodectiformes	*Saurodon**	2	Sa–Ma
Istiophoriformes	*Xiphias*	1	Pa
Kurtiformes	*Apogonidarum*	1	Pa
Labriformes	*Phyllodus*	1	Pa
Lepisosteiformes	*Atractosteus*	1	Ca
Ophidiiformes	*Bidenichthys*	1	Pa
Ophidiiformes	*Dinematichthys*	1	Pa
Ophidiiformes	*Ogilbia*	1	Pa
Ophidiiformes	*Fierasferoides*	1	Pa
Ophidiiformes	*Onuxodon*	1	Pa
Ophidiiformes	*Ampheristus*	1	Pa
Ophidiiformes	*Gadophycis*	1	Pa
Ophidiiformes	*Hoplobrotula*	1	Pa
Ophidiiformes	*Preophidion*	1	Pa
Osteoglossiformes	*Brychaetus*	1	Ma–Pa
Osteoglossiformes	*Genartina*	1	Pa
Pachycormiformes	*Belonostomus**	1	Ma
Pachycormiformes	*Protosphyraena*	2	Ce–Ma
Perciformes	*Scorpaena*	1	Pa
Perciformes	*Palaeopercichthys*	1	Pa
Pycnodontiformes	*Hensodon*	1	Ce
Pycnodontiformes	*Palaeobalistum*	1	Ma
Pycnodontiformes	*Nursallia*	1	Ce
Pycnodontiformes	*Palaeobalistum*	1	Ce
Pycnodontiformes	*Akromystax*	1	Ce
Pycnodontiformes	*Anomoeodus*	3	Sa–Ma
Pycnodontiformes	*Athrodon*	1	Ce
Pycnodontiformes	*Gyrodus*	1	Ce
Pycnodontiformes	*Micropycnodon*	1	Ce- Ca
Pycnodontiformes	*Phacodus*	1	Sa

Pycnodontiformes	*Polazzodus*	1	Sa
Pycnodontiformes	*Proscincetes*	1	Ce
Pycnodontiformes	*Pycnodus*	1	Sa–Pa
Scombriformes	*Sphyraenodus*	1	Pa
Scombriformes	*Cybium*	1	Pa
Scombriformes	*Mupus*	1	Pa
Semionotiformes	*Agoultichthys*	1	Ce
Semionotiformes	*Hadrodus*	1	Sa–Pa(?)
Siluriformes	*Arius*	1	Pa
Spariformes	*Nemipterus*	1	Pa
Tetraodontiformes	*Eotrigonodon*	1	Ma
Tetraodontiformes	*Ostracion*	1	Pa
Tetraodontiformes	*Stephanodus*	3	Ca–Ma
Tetraodontiformes	*Ostracion*	1	Ma
Tetraodontiformes	*Stephanodus*	1	Ma
Tselfatiiformes	*Bananogmius*	3	Sa–Pa(?)
Alepisauriformes	*Apateodus*	1	Sa
Acanthomorphata	*Sphyraena*	1	Ma
Acanthomorphata	*Acropoma*	1	Pa
Acanthomorphata	*Mene*	1	Pa
Acanthomorphata	*Pogonias*	3	Ce
Acanthopterygii	*Gigapteryx*	1	Ce
Sarcopterygi			
Coelacanthiformes	*Macropoma*	1	Ce–Sa
Coelacanthiformes	*Mawsonia*	1	Ce
Coelacanthiformes	*Megalocoelacanthus*	1	Sa–Ma

(c). Reptiles

Sauropsida	Genus	#s of species	Age
Plesiosauria - Elasmosauridae	*Albertonectes*	1	Ca
Plesiosauria - Elasmosauridae	*Alzadasaurus*	1	Ca
Plesiosauria - Elasmosauridae	*Aphrosaurus*	1	Ma
Plesiosauria - Elasmosauridae	*Aristonectes*	2	Ca - Ma
Plesiosauria - Elasmosauridae	*Cimoliasaurus*	2	Ce - Pa
Plesiosauria - Elasmosauridae	*Discosaurus*	1	Sa
Plesiosauria - Elasmosauridae	*Elasmosaurus*	7	Sa - Ma
Plesiosauria - Elasmosauridae	*Fresnosaurus*	2	Sa - Ma
Plesiosauria - Elasmosauridae	*Futabasaurus*	1	Sa
Plesiosauria - Elasmosauridae	*Hydrotherosaurus*	1	Ma
Plesiosauria - Elasmosauridae	*Libonectes*	1	Sa
Plesiosauria - Elasmosauridae	*Mauisaurus*	1	Sa - Ma
Plesiosauria - Elasmosauridae?	*Morenosaurus*	1	Ma
Plesiosauria - Elasmosauridae?	*Ogmodirus*	1	Sa
Plesiosauria - Elasmosauridae	*Scanisaurus*	1	Ca
Plesiosauria - Elasmosauridae	*Styxosaurus*	1	Sa - Ca
Plesiosauria - Elasmosauridae	*Terminonatator*	1	Ca
Plesiosauria - Elasmosauridae	*Thalassomedon*	1	Ce
Plesiosauria - Elasmosauridae	*Tuarangisaurus*	1	Ma
Plesiosauria - Elasmosauridae	*Zarafasaura*	1	Ma
Plesiosauria - Polycotylidae	*Dolichorhynchops*	2	Sa - Ca
Plesiosauria - Polycotylidae	*Eopolycotylus*	1	Ce
Plesiosauria - Polycotylidae	*Georgiasaurus*	1	Sa
Plesiosauria - Polycotylidae	*Manemergus*	1	Sa
Plesiosauria - Polycotylidae	*Pahasapasaurus*	1	Ce
Plesiosauria - Polycotylidae	*Palmulasaurus*	1	Sa
Plesiosauria - Polycotylidae	*Plesiopleurodon*	1	Ce
Plesiosauria - Polycotylidae	*Polycotylus*	1	Sa - Ca
Plesiosauria - Polycotylidae	*Thililua*	1	Sa
Plesiosauria - Polycotylidae	*Trinacromerum*	2	Ce - Ca
Plesiosauria - Pliosauridae	*Brachauchenius*	1	Ce - Sa
Plesiosauria - Pliosauridae	*Megacephalosaurus*	1	Sa
Plesiosauria - Pliosauridae	*Polyptychodon*	2	Ce - Sa
Plesiosauria - Pliosauridae	*Embaphias*	1	Ca
Plesiosauria - Pliosauridae	*Taphrosaurus*	1	Ce
Mosasauroidea	*Aigialosaurus*	2	Ce
Mosasauroidea	*Carentonosaurus*	1	Ce
Mosasauroidea	*Coniasaurus*	3	Ce
Mosasauroidea	*Dolichosaurus*	1	Ce
Mosasauroidea	*Tethysaurus*	1	Sa
Mosasauridae	*Amphekepubis*	1	Sa
Mosasauridae	*Angolasaurus*	1	Sa - Ma
Mosasauridae	*Carinodens*	2	Ma
Mosasauridae	*Clidastes**	3	Sa - Ca
Mosasauridae	*Dollosaurus*	1	Sa - Ca
Mosasauridae	*Ectenosaurus*	1	Sa
Mosasauridae	*Eidolosaurus*	1	Ce
Mosasauridae	*Eonatator*	2	Ca
Mosasauridae	*Eremiasaurus*	1	Ma
Mosasauridae	*Globidens*	3	Ca - Ma
Mosasauridae	*Goronyosaurus*	1	Ma

Mosasauridae	*Hainosaurus*	4	Ca - Ma
Mosasauridae	*Halisaurus*	4	Sa - Ma
Mosasauridae	*Igdamanosaurus*	1	Ma
Mosasauridae	*Kourisodon*	1	Sa - Ma
Mosasauridae	*Latoplatecarpus*	1	Ca
Mosasauridae	*Mosasaurus*	6	Ca - Ma
Mosasauridae	*Phosphorosaurus*	1	Ma
Mosasauridae	*Platecarpus*	4	Sa - Ma
Mosasauridae	*Plioplatecarpus*	5	Ca - Ma
Mosasauridae	*Plotosaurus*	2	Ma
Mosasauridae	*Pluridens*	1	Ma
Mosasauridae	*Prognathodon*	11	Ca – Ma
Mosasauridae	*Romeosaurus*	2	Sa
Mosasauridae	*Russellosaurus*	1	Sa
Mosasauridae	*Selmasaurus*	2	Sa – Ca
Mosasauridae	*Taniwhasaurus*	2	Ca – Ma
Mosasauridae	*Tylosaurus**	4	Sa – Ca
Mosasauridae	*Yaguarasaurus*	1	Sa
Serpentes(?)	*Haasiophis*	1	Ce
Serpentes	*Pachyrhachis*	1	Ce
Testudines - Bothremydidae	*Chedighaii*	1	Sa – Ca
Testudines - Bothremydidae	*Chupacabrachelys*	1	Ca
Testudines - Bothremydidae	*Elochelys*	1	Ca – Ma
Testudines - Bothremydidae	*Foxemys*	2	Sa – Ma
Testudines - Bothremydidae	*Kurmademys*	1	Ma
Testudines - Bothremydidae	*Labrostochelys*	1	Pa
Testudines - Bothremydidae	*Nigeremys*	2	Ca – Ma
Testudines - Bothremydidae	*Polysternon*	2	Sa – Ma
Testudines - Bothremydidae	*Taphrosphys*	3	Ca – Pa
Testudines - Bothremydidae	*Acleistochelys*	1	Pa
Testudines - Bothremydidae	*Araiochelys*	1	Pa
Testudines - Bothremydidae	*Arenila*	1	Ma
Testudines - Bothremydidae	*Azabbaremys*	1	Pa
Testudines - Bothremydidae	*Bothremys*	4	Ca – Pa
Testudines - Bothremydidae	*Chedighaii*	1	Ca
Testudines - Bothremydidae	*Podocnemis*	1	Ce
Testudines - Bothremydidae	*Polysternon*	1	Ce & Ma(?)
Testudines - Bothremydidae	*Rhothonemys*	1	Pa
Testudines - Bothremydidae	*Taphrosphys*	1	Ca - Pa
Testudines - Bothremydidae	*Zolhafah*	1	Ma
Testudines - Cheloniidae	*Allopleuron*	1	Sa - Ca
Testudines - Cheloniidae	*Ctenochelys*	3	Sa - Ca
Testudines - Cheloniidae	*Dollochelys*	1	Pa
Testudines - Cheloniidae	*Gigantatypus*	1	Ma
Testudines - Cheloniidae	*Itilochelys*	1	Pa
Testudines - Cheloniidae	*Nichollsemys*	1	Ca
Testudines - Cheloniidae	*Puppigerus*	1	Ce
Testudines - Cheloniidae	*Tasbacka*	3	Ma - Pa
Testudines - Dermochelyoidae	*Corsochelys*	1	Ca - Ma
Testudines - Dermochelyoidae	*Eosphargis*	1	Pa
Testudines - Dermochelyoidae	*Mesodermochelys*	1	Ca - Ma
Testudines - Dermochelyoidae	*Ocepechelon*	1	Ma
Testudines - Durocryptodira	*Toxochelys*	3	Sa - Ma(?)
Testudines - Eucryptodira	*Borealochelys*	1	Sa

Testudines - Kinosternoidea	*Agomphus*	3	Sa - Ma(?)
Testudines - Macrobaenidae	*Osteopygis*	6	Ma - Pa
Testudines - Macrobaenidae	*Aurorachelys*	1	Sa
Testudines - Nanhsiungchelyidae	*Anomalochelys*	1	Ce
Testudines - Pancheloniidae	*Euclastes*	3	Ma
Testudines - Pancheloniidae	*Lophochelys*	3	Ce - Pa
Testudines - Pancheloniidae	*Peritresius*	1	Ma - Pa
Testudines - Pancheloniidae	*Prionochelys*	3	Sa
Testudines - Pancheloniidae(?)	*Catapleura*	3	Ca - Pa
Testudines - Panpodocnemidae	*Shweboemys*	1	Sa
Testudines - Paracryptodira	*Angolachelys*	1	Sa
Testudines - Pleurosternidae	*Glyptops*	1	Ce
Testudines - Protostegidae	*Archelon*	1	Sa - Ma
Testudines - Protostegidae	*Calcarichelys*	1	Ma
Testudines - Protostegidae	*Chelosphargis*	1	Sa - Ma
Testudines - Protostegidae	*Desmatochelys*	1	Sa
Testudines - Protostegidae	*Protostega*	3	Ce - Ma
Testudines - Protostegidae	*Rhinochelys*	2	Ce - Sa
Testudines - Protostegidae	*Teguliscapha*	1	Ce
Testudines - Protostegidae	*Terlinguachelys*	1	Ca
Testudines - Protostegidae	*Brachyopsemys*	1	Pa
Testudines - Sinemydidae	*Judithemys*	1	Pa
Testudines - Thalassemydidae	*Rhetechelys*	1	Pa
Testudines - Trionychidae	*Amyda*	1	Ma
Testudines - Trionychidae	*Aspideretoides*	1	Pa
Testudines - Trionychidae	*Aspideretoides*	1	Pa
Testudines - Trionychidae	*Hummelichelys*	1	Ca
Testudines - Toxochelyidae	*Thinochelys*	1	Sa - Ma

6. References

1. Raymond, D. E., W. E. Osborne, C. W. Copeland, and T. L. Neathery. 1988. Alabama Stratigraphy. Geological Survey of Alabama Circular 40:1–97.
2. Jones, D. S., P. A., Mueller, J. R. Bryan, J. P. Dobson, J. E. T. Channell, J. C. Zachos, and M. A. Arthur. 1987. Biotic, geochemical, and paleomagnetic changes across the Cretaceous/Tertiary boundary at Braggs, Alabama. Geology 15:311–315.
3. Mancini, E. A. T. M. Puckett, B. H. Tew, and C. C. Smith. 1995. Upper Cretaceous sequence stratigraphy of the Mississippi – Alabama area. Gulf Coast Association of Geological Societies Transactions 45:377–384.
4. Ikejiri, T., J. Ebersole, H. L. Blewitt, and S. Ebersole. 2013. An overview of Late Cretaceous vertebrates from Alabama. Alabama Museum of Natural History Bulletin 31(1):46–71.
5. Ciampagalio, C. N., D. J. Cicimurri, J. A. Ebersole, and K. E. Runyon. 2013. A note on Late Cretaceous fish taxa recovered from stream gravels at Site AGr-43 in Greene County, Alabama. Alabama Museum of Natural History Bulletin 31-1:84–97.
6. Dunhill, A. M., M. J. Benton, R. J. Twitchett, and A. J. Newell. 2014. Testing the fossil record: Sampling proxies and scaling in the British Triassic–Jurassic. Palaeogeography, Palaeoclimatology, and Palaeoecology 404: 1–11.
7. Walker, F. M., A. M. Dunhill, M. A. Woods, A. J. Newell, and M. J. Benton. 2017. Assessing sampling of the fossil record in a geographically and stratigraphically constrained dataset: the Chalk Group of Hampshire, southern UK. Journal of the Geological Society 174: 509–521.
8. Alroy J. 2010a. Geographical, environmental and intrinsic biotic controls on Phanerozoic marine diversification. Palaeontology 53:1211–1235.
9. Mancini, E. A., B. H. Tew, and C. C. Smith. 1989. Cretaceous-Tertiary contact, Mississippi and Alabama. Journal of Foraminiferal Research 19:93–104.
10. Scotese, C. R. 2014. Atlas of Late Cretaceous Paleogeographic Maps, PALEOMAP Atlas for ArcGIS, volume 2, The Cretaceous, Maps 16 – 22, Mollweide Projection, PALEOMAP Project, Evanston, IL.
11. Carrano, M. T., J. Alroy, P. Mannion, and R. Benson. 2019. Taxonomic occurrences of Cretaceous to Paleocene Vertebrata recorded: *In*: Fossilworks, the Evolution of Terrestrial Ecosystems database, and the Paleobiology Database. http://fossilworks.org (January 2019).
12. Foote, M. 2000. Origination and extinction components of taxonomic diversity: general problems. Paleobiology 26 (sp4): 74–102.
13. Foote, M. & Miller, A. I. 2007. Principles of Paleontology Third Edition. W. H. Freeman and Company, 354 pp.