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Two pulses of morphological diversification in Pacific pelagic fishes following the Cretaceous–Palaeogene mass extinction

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Molecular phylogenies suggest some major radiations of open-ocean fish clades occurred roughly coincident with the Cretaceous–Palaeogene (K/Pg) boundary, however the timing and nature of this diversification is poorly constrained. Here, we investigate evolutionary patterns in ray-finned fishes across the K/Pg mass extinction 66 million years ago (Ma), using microfossils (isolated teeth) preserved in a South Pacific sediment core spanning 72–43 Ma. Our record does not show significant turnover of fish tooth morphotypes at the K/Pg boundary: only two of 48 Cretaceous tooth morphotypes disappear at the event in the South Pacific, a rate no different from background extinction. Capture–mark–recapture analysis finds two pulses of origination in fish tooth morphotypes following the mass extinction. The first pulse, at approximately 64 Ma, included short-lived teeth, as well as forms that contribute to an expansion into novel morphospace. A second pulse, centred at approximately 58 Ma, produced morphotype novelty in a different region of morphospace from the first pulse, and contributed significantly to Eocene tooth morphospace occupation. There was no significant increase in origination rates or expansion into novel morphospace during the early or middle Eocene, despite a near 10-fold increase in tooth abundance during that interval. Our results suggest that while the K/Pg event had a minor impact on fish diversity in terms of extinction, the removal of the few dominant Cretaceous morphotypes triggered a sequence of origination events allowing fishes to rapidly diversify morphologically, setting the stage for exceptional levels of ray-finned fish diversity in the Cenozoic.

1. Introduction

Fishes are the dominant group of aquatic vertebrates, with over 33 000 described species [1]. Over 90% of that species diversity is found within the ray-finned fishes (Actinopterygii) [1]. While actinopterygian history reaches back over 400 million years, most extant family-level lineages originated within the past 100 Ma [2–5]. Fossil and molecular evidence suggest that open-ocean fishes radiated following the Cretaceous–Palaeogene (K/Pg) mass extinction, expanding into novel morphospace and size classes in the early part of the Palaeogene [6–9]. However, it has been difficult to precisely

resolve the temporal relationship of the K/Pg mass extinction to the inferred radiation in open-ocean dwelling ray-finned fishes, due to large temporal uncertainties of molecular clocks and the sparse body fossil record.

There are reasons to suspect that the K/Pg mass extinction may have directly contributed to part of the Cenozoic radiation of ray-finned fishes. Mass extinction events have profoundly shaped the diversity of life on the planet [10–12], removing previously abundant taxa and allowing surviving lineages to diversify in their aftermath [13]. Following mass extinctions, there is often an interval of low diversity and high dominance assemblages, where one or two taxa account for most of the fossils present. These assemblages are eventually replaced by more complex and persistent ecosystems [14–16]. Ray-finned fishes have a history of survival across mass extinctions and diversification in the aftermath of ecological disaster [4,17]. The K/Pg event caused a selective extinction of large and fast-jawed predatory fishes [18], and both molecular and fossil data suggest that an ecologically diverse range of ray-finned fishes radiated afterward [7–9,19]. Further, it appears that open-ocean ray-finned fishes were disproportionately successful in maintaining and expanding their ecological dominance following the extinction event relative to other marine vertebrate groups such as sharks [6].

There are a number of significant palaeoclimatic events in the early Cenozoic which may have also played a role in shaping fish diversity following the K/Pg event. For example, the Palaeocene–Eocene Thermal Maximum (PETM), a period of rapid greenhouse-induced global warming and ocean acidification 56 Ma [20], had profound effects on marine and terrestrial ecosystems [20], and has been implicated in inferred extinction in some marine fish groups [21]. Here, we evaluate changes in morphological disparity and estimate rates of origination and extinction of open-ocean fish tooth morphotypes, a metric related to ecological and taxonomic diversity, across the K/Pg mass extinction and early Palaeogene climatic events through the middle Eocene, using a unique microfossil resource: isolated microfossil fish teeth (ichthyoliths) preserved in a deep-sea sediment core from the South Pacific Ocean. Such remains cannot, at present, be matched to specific taxonomic groups, though this is currently under investigation by Elizabeth Sibert. While some fish clades uniformly bear a common tooth morphotype, others display a wide range of dentitions even within a single genus, and some fishes have distinct tooth morphotypes within their oral and pharyngeal jaws. Regardless, teeth play a significant role in prey capture and handling, meaning that changes in tooth shape, size, and geometry likely represent a combination of both taxonomic and ecological shifts within fish communities. We use the terms 'diversity' and 'origination rates' of pelagic fishes throughout to refer to these morphotype-based metrics, as tooth shape can be a proxy for the dynamics of the group. Ichthyoliths are abundant in deep-sea sediment cores and can be studied at high temporal resolution, representing the most abundant and complete fossil record of fishes from the open ocean, complementing the more taxonomically informative but rare body fossils, and providing unique insights on marine vertebrate evolution from an ecosystem otherwise under-represented in the described fossil record.

(a) Two pulses of Palaeocene origination

Microfossil fish teeth are preserved in nearly all marine sediments but have often been overlooked by micropalaeontologists due to their small size and low abundance when compared to other microfossils. Ichthyolith morphotypes and assemblages exhibit distinct changes through strata and have been used for biostratigraphy, suggesting that these fossils capture evolutionary or ecological changes in fish communities through time [22,23]. To quantify this morphological variation, we developed a novel character-state coding system (see electronic supplementary material for details), and classified 1 897 teeth ranging in age from 72 to 43 Ma from Deep Sea Drilling Project (DSDP) Site 596, a red clay sediment core from the South Pacific gyre. We identified 136 unique tooth morphotypes, each defined as a unique combination of character-states. DSDP 596 has a prominent iridium anomaly at the K/Pg boundary [24], and an established age model based on cobalt accumulation rate and biostratigraphy [25]. Continuous sedimentation through the study interval and abundant ichthyoliths make DSDP 596 an ideal site for evolutionary studies of open-ocean fishes, as the site has remained within the gyre habitat throughout the past 85 million years [25]. Prior work at DSDP Site 596 has shown that there was an increase in the relative abundance of fishes at the K/Pg extinction, and a period of increased relative abundance of extremely large teeth spanning approximately 64 to 62 Ma [6]. These changes in the post-K/Pg ichthyolith assemblages are also observed in Ocean Drilling Program (ODP) Site 886, in the North Pacific gyre, as well as several locations in the North and South Atlantic [6], though hiatuses, limited sampling, and low tooth abundance preclude detailed morphological work at those sites.

The stratigraphic ranges of the identified ichthyolith morphotypes are presented in figure 1. No morphotypes in our dataset disappear in the Cretaceous prior to the K/Pg boundary. Further, similar to plankton groups (e.g. calcareous nannofossils [26]), there is no evidence for a drawn-out extinction or assemblage shifts in the latest Cretaceous [27], suggesting that any environmental change prior to the mass extinction was not a significant factor in driving changes in fish tooth diversity or community structure. Cretaceous assemblages were dominated by three morphotypes, which together commonly comprised approximately 50% of each assemblage (figure 1). Other late Cretaceous morphotypes were rarer, with only 1–2 teeth per morphotype in assemblages of 50–70 teeth. Only two of 48 Cretaceous morphotypes went extinct at the K/Pg event (approximately 4% extinction). However, these two morphotypes represented two of the three most abundant forms in the Late Cretaceous, so their extinction resulted in a marked change in assemblage composition. The third dominant Cretaceous morphotype persisted just two million years into the Palaeocene, but was present at much lower relative abundances than before the mass extinction.

Most of the remaining Late Cretaceous morphotypes persisted into the Palaeocene, many becoming more common than they were in the Cretaceous. The early Palaeocene fish assemblage shows higher evenness than the Cretaceous assemblage, with surviving morphotypes present at slightly elevated abundances when compared to novel Palaeocene forms. In contrast to the Cretaceous, no single morphotype
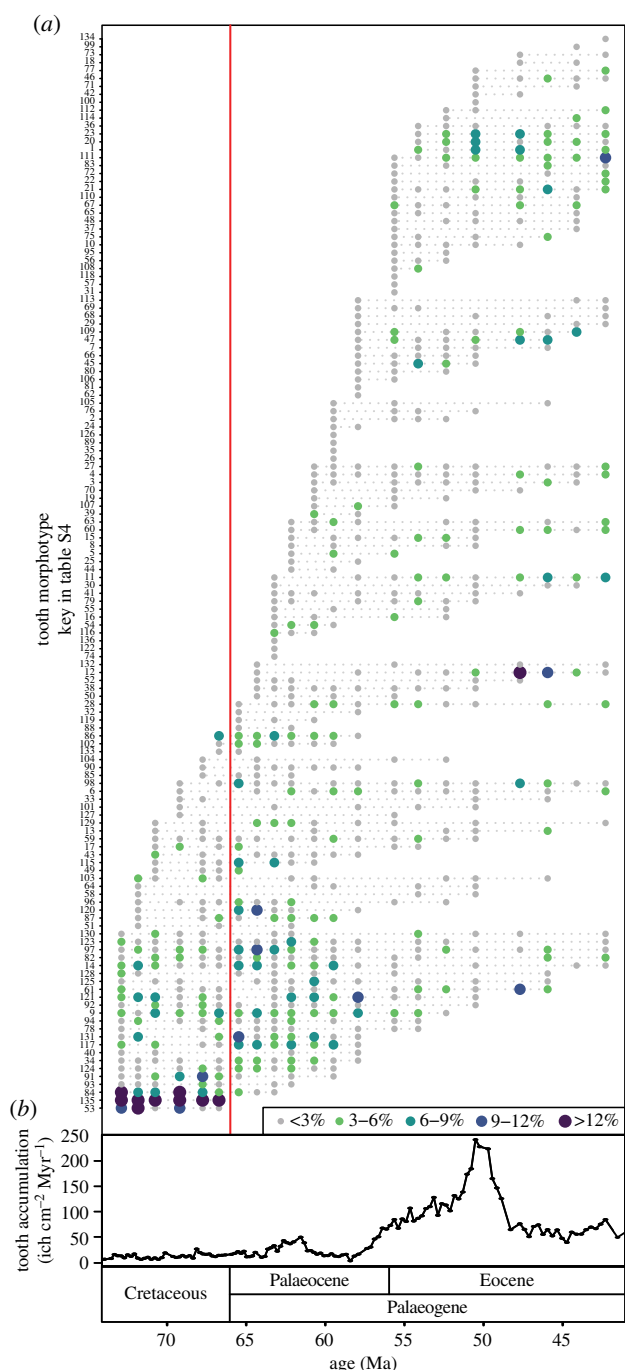
Figure 1. (*a*) Stratigraphic range chart of ichthyolith morphotype occurrences using the 'low reworking' dataset (see electronic supplementary material). Size and colour of dot represents the relative abundance of each morphotype observed in a time bin, with larger dots representing higher relative abundances of those fossils. The red horizontal line is the K/Pg boundary. The vertical axis is individual tooth morphotypes defined for this study, ordered by first occurrence then last occurrence age. A key for translating number to morphotype is in electronic supplementary material, table S4.

was present consistently at high relative abundance during the first half of the Palaeocene. Further, despite a nearly 8-fold increase in tooth accumulation rate in the early Eocene (figure 1*b*), relatively little tooth morphological novelty appeared during that interval. Instead, the majority of new morphotypes were first observed in the Palaeocene, which has consistently low numbers of total teeth in each sample. We suggest that the novelty observed in the Palaeocene is likely underestimated, masked by low tooth abundances. Together, these imply that the K/Pg event

disrupted the high-dominance structure of Late Cretaceous fish communities, likely facilitating the morphological diversification observed during the Palaeocene. Notably, this morphological diversification of tooth types does not continue into the Eocene, despite a massive increase in fish tooth abundance during that time. It is likely that the apparent Palaeocene radiation in pelagic fishes was linked to the ecological restructuring that followed the K/Pg extinction while the increase in Eocene tooth abundance was built on morphotypes that had already appeared in the Palaeocene.

To quantify the radiation of tooth morphotypes, we estimated origination and extinction probabilities using capture–mark–recapture (CMR). This method accounts for incomplete sampling by estimating the probability of detection and probability of survival for each morphotype throughout the study interval, by taking advantage of morphotypes which range through multiple time steps but are not detected in every sample in-between [28–30]. Traditional palaeontological methods (e.g. Boundary Crossers [31]) yield similar patterns for our data (see electronic supplementary material, discussion and figure S4). There is no obvious increase in extinction rate of fish tooth morphotypes associated with the K/Pg event, with the best-fit models estimating a near-constant 5% extinction probability per million years throughout the entire study interval (figure 2). However, there are two distinct peaks in morphotype origination following the extinction event, at 64 Ma and 58 Ma, respectively (figure 2). As both peaks in origination rate precede, rather than coincide with, peaks in absolute abundance of teeth, it is unlikely that our estimates of increased novelty are artefacts of increased sampling intensity. It is more likely that we underestimate the magnitude of morphological novelty during these intervals, as the absolute number of teeth observed during them is small (see electronic supplementary material, figure S2). Further, despite the relatively low abundances of teeth compared to the Eocene, the Palaeocene was a time of net origination of tooth morphotypes, with origination rate exceeding extinction rate. In contrast, the Eocene was a time of net extinction, while absolute abundance of teeth was greater than 5-fold that of Palaeocene levels, suggesting that evolutionary dynamics were distinctly different between the two epochs, and that high tooth accumulation is not correlated with high diversification rates.

Migration or shifts in geographical range might contribute to the peaks in novelty observed at this site. However, migration is unlikely to be the principal process underlying the patterns presented here. Migration includes both immigration (which could be confounded with origination) and emigration (which could be confounded with extinction). While there are distinct changes in origination rate, there is nothing in our extinction estimates consistent with large-scale emigration. Further, open-ocean fishes tend to have cosmopolitan distributions [1], making it geometrically more difficult for point occurrences to be governed by changes in range than for species with more restricted distributions.

The K/Pg extinction event is not associated with a decrease in fish tooth morphospace occupation. The vast majority of teeth in this study occupy a central region of the morphospace that does not change substantially during the study interval (figure 3). While the majority of origination in the Palaeogene occurred within already occupied morphospace, each of the Palaeocene origination pulses included an
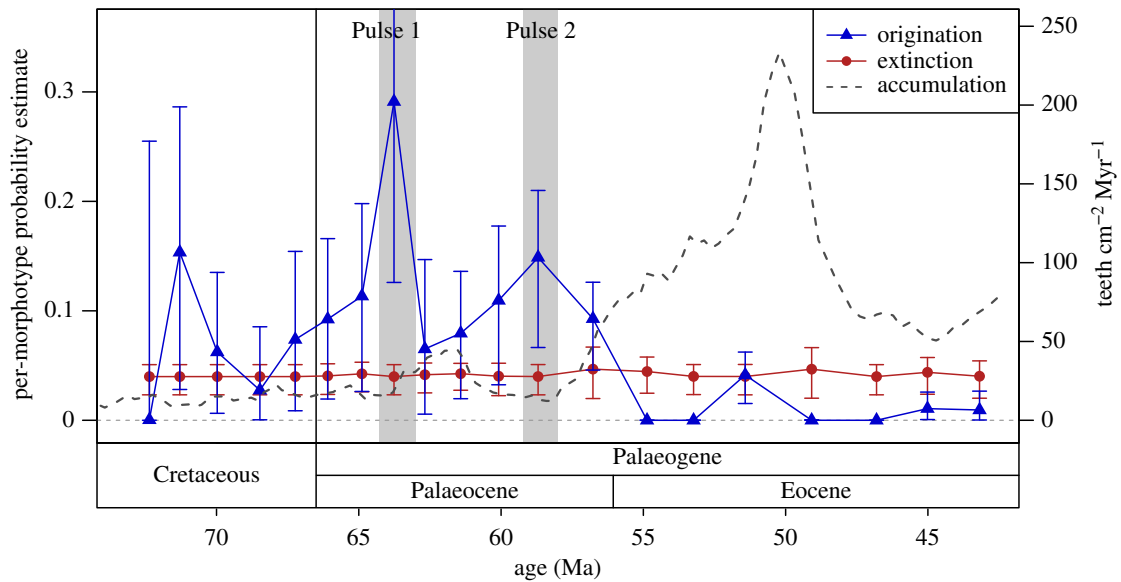
Figure 2. Origination and extinction rate estimates from the Pradel-recruitment capture–mark–recapture model (see electronic supplementary material figure S4 for all models and methods). Dark grey shaded regions represent the two non-zero pulses of origination observed. Red circles are extinction, while blue triangles are origination. Error bars are upper and lower confidence levels estimated by MARK. The grey dotted line shows absolute accumulation of fish teeth at the site.

expansion into a distinct region of previously unoccupied morphospace (figure 3). While both time periods produced short-lived, novel morphotypes, Pulse 1 included a higher number of morphologically extreme, short-lived morphotypes, and corresponds to a period of elevated relative abundance of extremely large teeth in both the North and South Pacific ocean basins [6]. This suggests that the two Palaeocene pulses of novel morphotypes were distinct from each other, possibly due to differing ecological and climatic conditions between the two intervals (figure 3). However, the novel morphotypes at the extremes of morphospace comprised a relatively small proportion of the total teeth in the assemblages, so fish represented by these extreme morphotypes may not have played a substantial ecological role in earliest Palaeocene ecosystems. Alternatively, as some fishes have more than one tooth morphotype present throughout their jaws and skulls, it is possible that these early Palaeocene fishes had only a small number of large, novel teeth, while also producing a larger number of less distinctive teeth, which would dilute the observed relative abundance of these morphotypes, contributing to their relative rarity in the assemblages. Despite these significant incursions into novel morphospace, the vast majority of teeth in the Late Cretaceous and early Palaeogene occurred within previously occupied regions of morphospace, suggesting that fishes were able to maintain their established tooth morphological diversity across the K/Pg event, at least in this region, potentially priming the group for the Palaeocene radiations observed here.

The timing of these pulses in morphological innovation in the South Pacific Ocean do not correlate with the known major environmental events of the early Palaeogene. For example, PETM, 56 Ma is associated with a significant extinction in benthic foraminifera [32], range contractions in calcareous nannofossils [33], and ocean acidification [34,35], as well as dwarfing and rapid turnover of mammal communities on land [36]. Extinction in tetraodontiform fishes at the PETM has been inferred from molecular phylogenies [21], although most members of this clade are associated with

shallow or coastal settings rather than the pelagic ones. Our data do not support evidence for a major turnover in open-ocean fishes at the PETM. The PETM occurred just after the second pulse of origination, so it is possible that the event put an end to the period of elevated morphotype origination in the late Palaeocene. However, as there is no significant turnover in tooth morphotypes between the late Palaeocene and early Eocene, our dataset does not support any clear negative impact of the PETM on the diversity of open-ocean fishes, at least in the South Pacific gyre.

In the South Pacific Ocean, rates of fish tooth accumulation reached peak values of more than five times higher than those in the Palaeocene or Cretaceous at approximately 50 Ma [37]. Peak tooth accumulation coincides with the Early Eocene Climate Optimum (EECO), a period of extreme global warmth [38]. Many plankton groups reached a peak in diversity during the early–middle Eocene [39,40], suggesting that this may have been a formative time for open-ocean biodiversity. However, while tooth abundance appears to increase and decrease in concert with bottom water temperature at DSDP Site 596 in the early Cenozoic [37], there is little origination in morphotype diversity or morphospace occupation during the interval. The Eocene is the only time within our record where extinction rate consistently exceeds origination. Estimated rates of extinction, however, are not significantly higher in the Eocene than during the rest of the record: if anything, this period of extreme greenhouse warmth and high fish abundance is associated with reduced origination in pelagic fishes. It is possible that the reduced origination rates in the Eocene may be in part due to diversity-dependence or ecological saturation of extant morphotypes, as it occurs following a period of increased origination and high standing morphological diversity, a phenomenon previously observed in planktonic foraminifera throughout the Cenozoic [41].

It is possible that considerable origination and extinction occurred during the early Palaeogene climatic events that is not observed in our dataset. Tooth morphology is determined by a combination of function and phylogenetic history, and
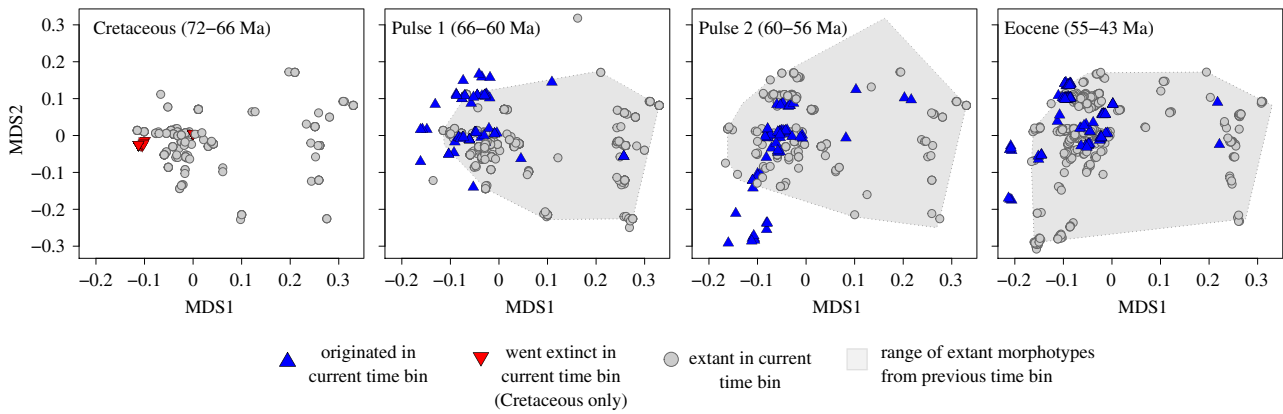
Figure 3. Morphospace occupation of tooth morphotypes from the Cretaceous, Pulse 1, Pulse 2, and Eocene time bins, showing dimensions 1 and 2 of a 3-dimensional non-metric multi-dimensional scaling (NMDS) analysis (stress = 0.11). Blue upwards triangles represent morphotypes which originated in that time bin. Red triangles in the Cretaceous represent the two morphotypes which went extinct at the K/Pg event. Grey circles represent morphotypes which originated in a prior time bin and are present in the current time bin. The grey shaded region is the occupied morphospace from the prior time bin, to facilitate comparison of novel morphotypes and morphospace occupation changes between time intervals. Most morphotypes are centred around (0,0) on the MDS1 and MDS2 axes.

the morphotypes defined here likely represent higher order taxonomic or ecological groupings than species. For example, the average duration of a tooth morphotype in this record is approximately 12 million years, which is considerably longer than the estimated species duration for freshwater fishes, approximately 3 million years [42], and is at the upper end of the range for marine invertebrate species, which have been estimated to last between 5 and 12 million years [43]. As such, it is possible that considerable speciation and extinction occurred within already extant genera, families, or ecological guilds, which may not be observable in these teeth or at this location. However, even if this is the case, the evolutionary changes throughout the Palaeocene were greater than observed shifts that occurred during the other parts of this record, including across the PETM and during the early Eocene. This suggests that the K/Pg event catalysed a radiation within the group that occurred largely during the Palaeocene and was finished by the early Eocene, defining the morphological and ecological role of fishes into the early Cenozoic.

2. Conclusion

The K/Pg extinction did not produce a large change in the morphological diversity of the latest Cretaceous open-ocean fish community, but did remove some of the most abundant forms and reduced the dominance in tooth morphotype assemblages. In the aftermath of the extinction, there were two distinct pulses of origination during the Palaeocene in the South Pacific, at 64 and 58 Ma, each expanding into a different region of previously unoccupied morphospace. While the first pulse or origination was likely a direct response to the K/Pg event, the mechanism behind the second pulse remains unclear: as there is no obvious climatic driver, it may have been driven in part by ecological restructuring as other marine groups recovered from the event. Further, while there was a peak in abundance of fish teeth during the early Eocene, there was very little origination of novel tooth morphotypes during that interval. This is in contrast to the patterns observed in other open-ocean plankton groups, such as planktonic foraminifera which have an initial radiation in the early Palaeocene, but do not reach peak diversity until the early/middle Eocene [40]. However, the

patterns of extinction for fish and foraminifera are nearly opposite: while the fishes saw an extinction of only two morphotypes of 48 at the K/Pg event, only three species of planktonic foraminifera out of 50 are thought to have survived the extinction event. Calcareous nannofossils, which also suffered considerable extinction at the K/Pg event reach peak diversity in the middle to late Eocene [39]. Fishes were likely able to respond rapidly in the aftermath of the extinction event in part because they retained their standing tooth morphotype diversity and existing morphospace occupation across the K/Pg event. In addition, the extinction of other abundant pelagic consumers, including ammonites [44], may have opened up opportunities for the surviving fish lineages. The disruption of the high-dominance Cretaceous fish tooth assemblages, with a small but ecologically significant extinction in fish tooth morphological diversity at the K/Pg boundary, combined with the rapid pace of diversification in the early Palaeocene suggests that overall, the K/Pg extinction event and the conditions of the Palaeocene allowed fishes to diversify rapidly following the extinction event, laying the foundation for the high Cenozoic levels of diversity in the clade.

3. Methods summary

(a) Sample preparation

Ichthyoliths were isolated from discrete sediment samples from DSDP Site 596, a red-clay sediment core from the South Pacific gyre, following standard protocols for ichthyolith isolation and preparation [45]. DSDP 596 has a well-constrained age model for a red clay site, with a prominent iridium anomaly at the K/Pg event [24], a cobalt-accumulation based age model [25], and additional biostratigraphic tie points [46]. To facilitate ichthyolith description, ichthyolith assemblages were imaged at high resolution (approx. 1 μm pixel^{-1}), and measured using the Hull Lab Imaging System and *AutoMorph* software at Yale University [47]. Individual teeth which appeared to be obviously reworked were removed from some analyses, to assess the impact of reworking. Our results were robust to a variety of reworking scenarios, and main text figures show the intermediate 'low reworking' results (see electronic supplementary material for details).

(b) Morphological disparity

Fish teeth have distinct morphological shapes that are likely a combination of taxonomic history and ecological role, and which exhibit distinct stratigraphic ranges (figure 1). To quantify morphological variation in these microfossils, we developed and employed a character-based coded system to create a non-hierarchical, 'taxon-free' morphological classification based on prior ichthyolith work [22,23,48–52], updated to include additional morphological diversity, and to use reflected, rather than transmitted light microscopy (see electronic supplementary material for details of the full coding scheme and electronic supplementary material, figure S1 for a visual summary of the characters considered). For this study, we defined any tooth that had a unique set of character-states as a distinct morphotype: 136 unique tooth morphotypes were identified and given descriptive in-house names to facilitate analysis. As our character-coding system is non-hierarchical, we felt this splitting of morphotypes was the most reasonable way to consider tooth types without introducing a potentially false hierarchy into the system.

(c) Evolutionary rate calculations

Evolutionary rates were evaluated using capture–mark–recapture methods. Analyses were carried out in R [53] using the package RMark [54] as an interface with MARK [55], a maximum-likelihood capture–mark–recapture calculation software. We used the Pradel 1996 [29] formulation of CMR, which can used to simultaneously estimate extinction and origination. We present results of the Pradel-Recruitment model formulation [55], as this is a model often used in palaeontological studies [28]. These results were compared with more traditional 'boundary crosser' metrics [31] on the same dataset, and both show similar patterns. Please see electronic supplementary material for additional discussion and electronic supplementary material, figure S4 for a comparison of all estimated origination and extinction rates.

(d) Morphological disparity analysis

All analyses were carried out using the R Statistical Package [53]. Using the morphological coding system, we calculated dissimilarity between each fossil in the dataset, using a custom R function that allowed for nonlinear dissimilarity between character-states within each character (see electronic supplementary material for additional details), to reduce the likelihood of introducing false hierarchy into the analysis. This dissimilarity matrix was visualized using a 3-dimensional non-metric multidimensional scaling (NMDS) analysis (stress = 0.11) using the R package vegan [56]. To facilitate visualization, the samples were grouped into time intervals of: Cretaceous (greater than 66 Ma), Palaeocene Pulse 1 (66–60 Ma), Palaeocene Pulse 2 (60–56 Ma), and Eocene (less than 56 Ma). All data, distance matrices, and code are available at www.github.com/esibert/toothmorph.

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