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Comment on "An early Miocene extinction in pelagic sharks"

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Abstract: Sibert and Rubin (Research Articles, 4 June 2021, p. 1105) recently claimed a previously unidentified, major extinction event of open-ocean sharks in the early Miocene. However, their interpretations are based on a flawed experimental design that does not account for a considerable rise in the sedimentation rate coinciding with the proposed event or intraspecific variation in denticle morphology.

One-Sentence Summary: We refute the suggestion of an early Miocene shark extinction event, and suggest that this perceived event is an artefact due to sampling technique.

Main Text: Deep-sea sediments comprising traces of ancient life carry fundamental information about the global ecosystem vital for understanding the driving forces of biodiversity through deep time. While many diversity studies of fossil sharks are based exclusively on teeth, Sibert and Rubin (*1*) use fossil dermal denticles of elasmobranchs to describe ancient diversity patterns. Based on the fossil record of dermal denticles of unidentified elasmobranchs and teeth of unidentified bony fishes collected from not more than a few grams per sediment sample, the authors identify a drastic extinction event in the early Miocene that nearly wiped out the open-ocean shark community during this time (Fig. 1A). We present here two major concerns pertaining to the quantity and quality of their data that led them to propose a hypothesis that cannot be supported.

Our first concern regards the sampling method. Sibert and Rubin (*1*) based their analyses on one core from the South Pacific Ocean (DSDP Site 596) and one from the North Pacific (OPD Site 886). However, the latter core should be excluded due to a hiatus horizon between 22.4 Ma and 11.5 Ma that spans the supposed extinction.

Sibert and Rubin (*1*) discuss sedimentation rates only briefly when referring to "increased variability in the sediment composition and sedimentation rate at DSDP Site 596, indicating higher variability in the depositional environment". However, the alleged extinction event perfectly aligns with a major increase in the sedimentation rate (*2*) (Fig. 1B). Interestingly, it also coincides with a severe abundance drop in the accompanying bony fish fauna, which is not recognized by the authors (Fig. 1C). The increased sedimentation from 20 Ma onwards causes a strongly diluted fossil concentration, but the authors did not correct for this artifact by analyzing larger sample sizes. Instead, they used similar amounts of samples throughout the study interval (mean 8.51 g from 0–19.75 Ma versus 8.04 g from 19.75–41.77 Ma).

From 19.75 Ma to 41.77 Ma, predating the assumed extinction event, we observe a rather constant and predictable offset between the number of bony fish fossils and detected elasmobranch denticles (Fig. 1C). Bony fish fossils and elasmobranch denticles are highly and significantly correlated in that interval (0.893, $P < 0.001$), suggesting an almost stable relationship between individual abundances of sharks and bony fish. Sibert and Rubin (*1*) correctly observed that this ratio changed significantly after the assumed extinction event. The shift in the ratio is, however, a statistical artifact from the numerator (i.e., the number of denticles) being zero or close to it. As such, any ratio becomes meaningless.

We test the null hypothesis that the relationship between bony fish and shark fossils is the same before and after the presumed extinction event. We calculated the mean ratio between bony fish fossils and elasmobranch denticles across all samples from the interval 19.75–41.77 Ma to evaluate how many bony fish fossils need to be present in a sample to expect at least one elasmobranch denticle. This calculation results in a minimum of 6.54 bony fish fossils per dermal denticle (standard deviation = 4.17). Especially when we look at the interval following the assumed event, only three samples marginally exceed the upper threshold (mean plus one standard deviation). In contrast, most samples contain too few specimens to allow any reconstruction of species richness or the denticle/tooth ratio. Also, the sample defining the end of the event is with 12 fish teeth only slightly above the threshold, casting doubt on the reliability of the authors' interpretation (Fig. 1D).

Our second concern refers to the usage of dermal denticles to reconstruct shark paleobiodiversity fluctuations. This approach is generally problematic due to the high variation of morphotypes within species, ontogenetic stages, possibly different sexes and even single individuals (*3, 4, 5*).

The authors assumed a low degree of variation (e.g., one or two morphotypes per species), but without any well-founded explanation. To demonstrate the morphological variability, we show as an example the dermal denticles from different body regions of a single individual of a deep-sea shark, *Etmopterus pusillus* (smooth lantern shark: Fig. 2A–J). Further examples of denticle variation in different species and body regions are known from the literature (*3–9*). The intrageneric differences in denticle morphology of some genera of oceanic sharks (such as *Etmopterus* and *Centrophorus*) is dramatic, spanning both main categories used here. However, Sibert and Rubin (*1*) compared denticles of only 27% of extant species, and there is no indication as to the degree of intraspecific denticle variation was accounted for. We conclude that the extinct geometric morphotypes from DSDP (Site 596), listed by Sibert and Rubin (*1*) as "4, 6, 23, 28, 29, 35, 41, 42, 57–60, 64, 65, 69 and 87", could actually belong to a single genus. The intraspecific variability of morphotypes in combination with unknown shedding rates and body sizes make solitary dermal denticles not a reliable proxy for species richness.

The alleged extinction event is additionally challenged by a comprehensive global analysis of the tooth-based fossil record of elasmobranchs on genus-level, demonstrating a stable genus richness of both oceanic and inshore groups throughout the early Miocene (*10*, *11*).

Our knowledge regarding the elasmobranch fauna of the ancient open-ocean realm probed by the DODP and ODP is still limited. Sibert and Rubin (*1*) applied sophisticated approaches to contribute to our knowledge about this unexplored but crucial environment. However, the underlying data do not support ~~a drastic~~ extinction event, which is supposedly substantially greater than the K/Pg event and exclusively affected sharks. Besides the possibility of local extinction, a faunal turnover could also affect a change in dermal denticle morphology and frequency. Consequently, we reject Sibert and Rubin's hypothesis due to the underestimated impact of the experimental design and insufficient sampling strategy by failing to consider changing sedimentation rates and intraspecific morphological variation of denticles.

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Methodology: IF, TAN, MH

Writing – original draft: IF, JP, NS, TAN, MH

Editing: IF, SA, GC, GG, JK, RAN, JP, KS, NS, CU, RV, MH

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Data and materials availability: Original and updated datasets from (*1, 2*).

Fig. 1. Data of Sibert and Rubin reinterpreted. The assumed extinction event is indicated by the horizontal grey bar. (**A**) Accumulation curves and denticle/tooth ratio as in Figure 1 of Sibert and Rubin. (**B**) Sedimentation rate (*2*) shifted by 0.36 Myr as in Sibert and Rubin to correct for the updated age of the K/Pg boundary. Note the distinct rise in the rate at the assumed event. (**C**) Number of denticles/teeth per gram sample weight. Note the nearly constant offset between the number of elasmobranch denticles (red) and bony fish teeth (gray) prior to the assumed event. (**D**) Number of elasmobranch denticles and bony fish teeth for the interval following the assumed event (log10-transformed). The vertical lines indicate the mean and one standard deviation of the empirical minimum number of bony fish teeth required to detect at least one denticle (calculated based on the pre-extinction interval).

Fig. 2. Denticle morphotype variation within a single individual. The high degree of denticle variation of the extant smooth lanternshark, *Etmopterus pusillus* (syntype, NHMW-78526.5, from Yokohama, Japan) including the following shapes that can be found on different body

regions: (**A–H**) Star- to square-like shapes; (**I–J**) Elongated rectangles to spear-head forms and (**I**) Denticles with additional ridges. Scale bars equal 100 µm, except E and I (200µm).

Fig. 1.

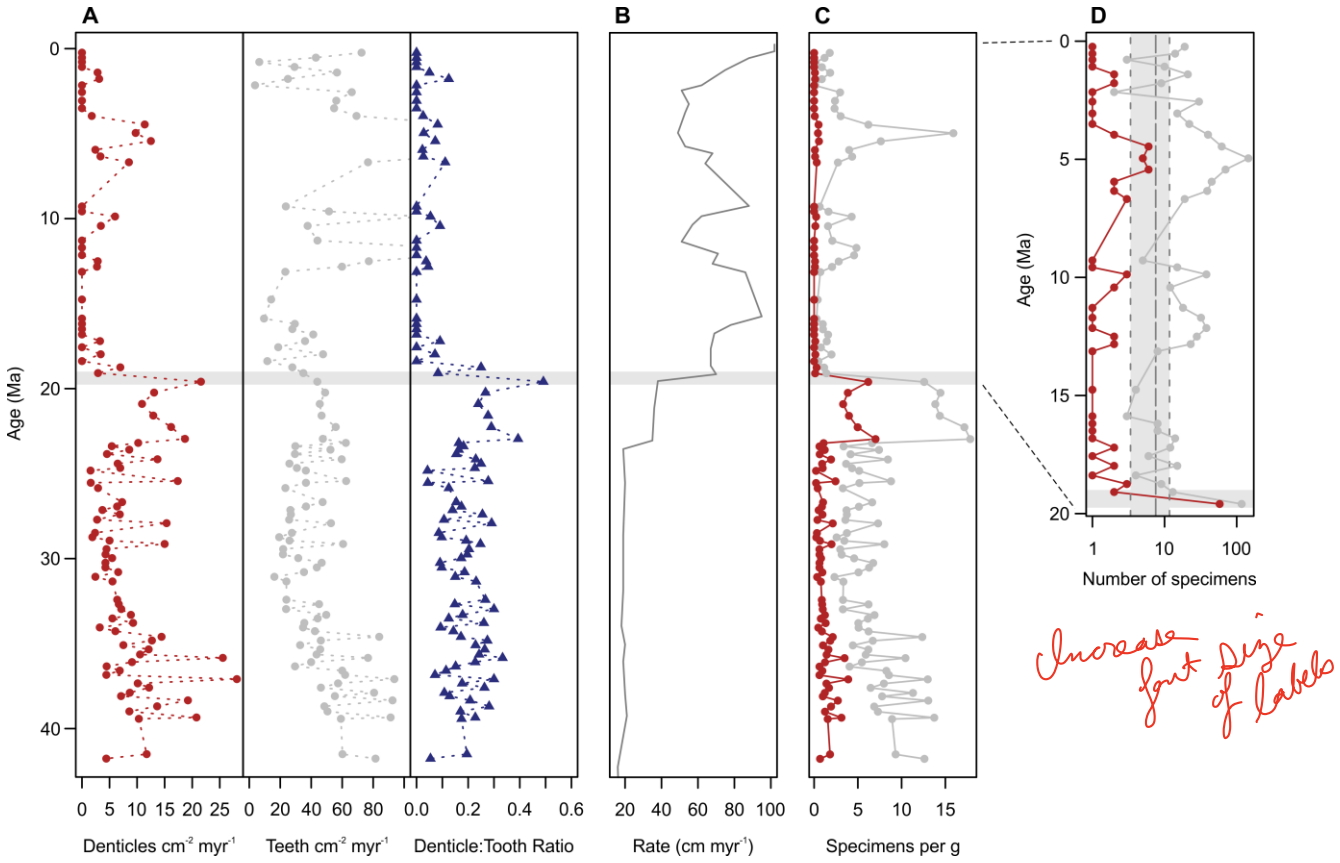
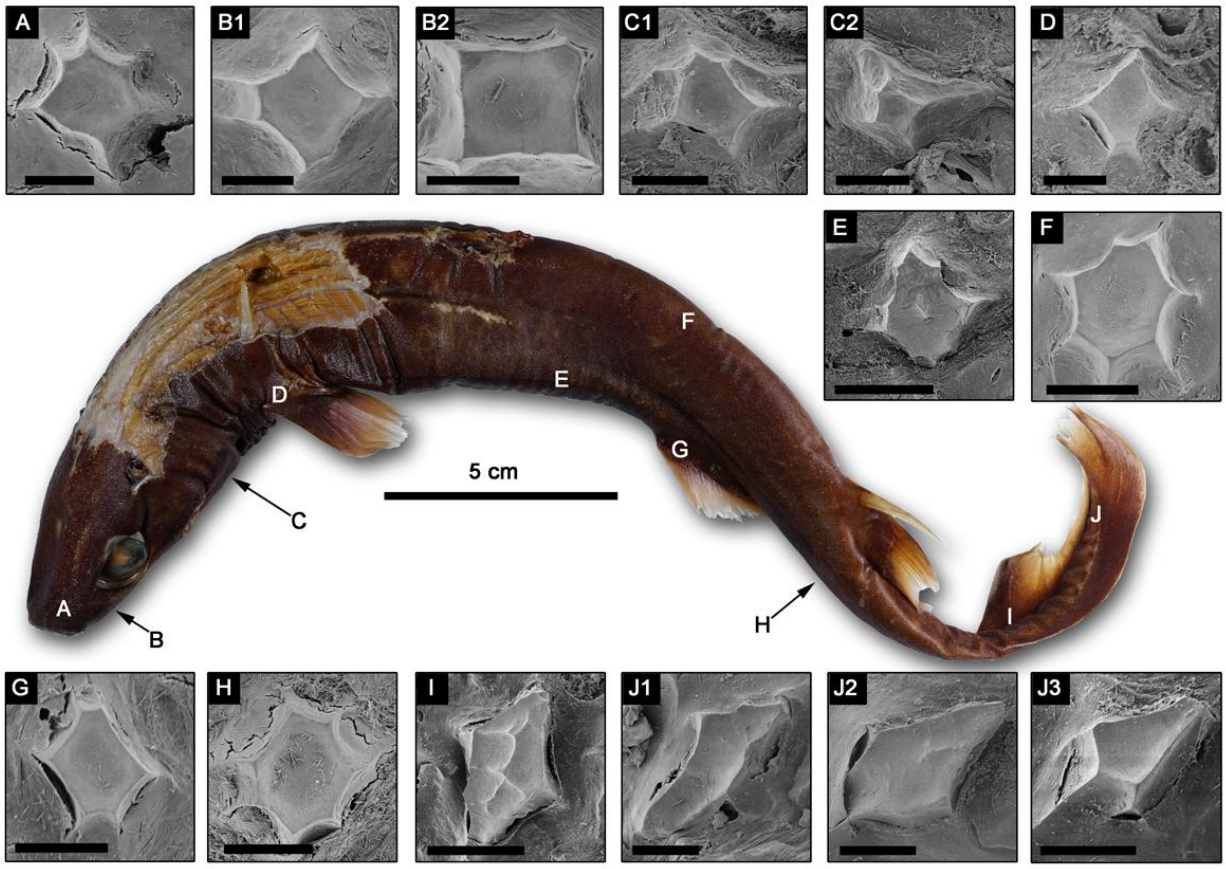
Fig. 2