

Rapid recovery of life at ground zero of the end-Cretaceous mass extinction

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The Cretaceous/Palaeogene mass extinction eradicated 76% of species on Earth^{1,2}. It was caused by the impact of an asteroid^{3,4} on the Yucatán carbonate platform in the southern Gulf of Mexico 66 million years ago⁵, forming the Chicxulub impact crater^{6,7}. After the mass extinction, the recovery of the global marine ecosystem—measured as primary productivity—was geographically heterogeneous⁸; export production in the Gulf of Mexico and North Atlantic–western Tethys was slower than in most other regions^{8–11}, taking 300 thousand years (kyr) to return to levels similar to those of the Late Cretaceous period. Delayed recovery of marine productivity closer to the crater implies an impact-related environmental control, such as toxic metal poisoning¹², on recovery times. If no such geographic pattern exists, the best explanation for the observed heterogeneity is a combination of ecological factors—trophic interactions¹³, species incumbency and competitive exclusion by opportunists¹⁴—and ‘chance’^{8,15,16}. The question of whether the post-impact recovery of marine productivity was delayed closer to the crater has a bearing on the predictability of future patterns of recovery in anthropogenically perturbed ecosystems. If there is a relationship between the distance from the impact and the recovery of marine productivity, we would expect recovery rates to be slowest in the crater itself. Here we present a record of foraminifera, calcareous nannoplankton, trace fossils and elemental abundance data from within the Chicxulub crater, dated to approximately the first 200 kyr of the Palaeocene. We show that life reappeared in the basin just years after the impact and a high-productivity ecosystem was established within 30 kyr, which indicates that proximity to the impact did not delay recovery and that there was therefore no impact-related environmental control on recovery. Ecological processes probably controlled the recovery of productivity after the Cretaceous/Palaeogene mass extinction and are therefore likely to be important for the response of the ocean ecosystem to other rapid extinction events.

The recent joint expedition of the International Ocean Discovery Program and International Continental Drilling Program (hereafter,

Expedition 364) recovered what is, to our knowledge, the first record of the few hundred thousand years immediately after the impact within the Chicxulub crater. Site M0077, which was drilled into the peak ring of the crater⁷ (Extended Data Fig. 1), sampled an approximately 130-m-thick, generally upward-fining suevite (that is, melt-bearing impact breccia) overlying impact melt rocks and fractured granite¹⁷. The boundary between the suevite and overlying earliest-Palaeocene pelagic limestone is in core 40-1 (Fig. 1), and comprises a 76-cm-thick upward-fining, brown, fine-grained micritic limestone that we term the ‘transitional unit’. The lower portion of the transitional unit is laminated below 54-cm core depth and contains no trace fossils (Fig. 1 and Extended Data Fig. 2). The laminations are thin, graded beds with sub-millimetre-scale cross-bedding that indicates bottom currents, and are likely due to the movement of wave energy—including tsunami and/or seiches—in the days after the impact. The fine grain size (primarily clay to silt, with some sand-sized grains concentrated in the graded beds) suggests that much of the material in the transitional unit was deposited from resuspension and settling. The transitional unit is overlain by a white pelagic limestone. The lowermost sample taken in this limestone (34 cm core depth) contains the planktic foraminifer *Parvularugoglobigerina eugubina* (which marks the base of Zone P α), other foraminifer of the same genus (*P. extensa*, *P. alabamensis*) and *Guembelitra cretacea*. Because many other species that originate within Zone P α first appear a few centimetres higher in the section (31–32 cm), we conclude that the base of the limestone lies very near the base of this zone, 30 kyr after the impact¹⁸.

Biostratigraphy and basic assumptions about depositional and crater processes indicate that the transitional unit was deposited between several years and 30 kyr after impact (Fig. 2). To better constrain this, we use the abundance of extraterrestrial ³He to determine sediment accumulation rates (see Methods). This proxy provides a firm upper limit of 8 kyr for deposition, assuming none of the ³He is reworked. If even a small amount of ³He is reworked (which is very likely given the prevalence of reworked microfossils and impact debris), then the transitional unit was deposited in a period of time of less than about

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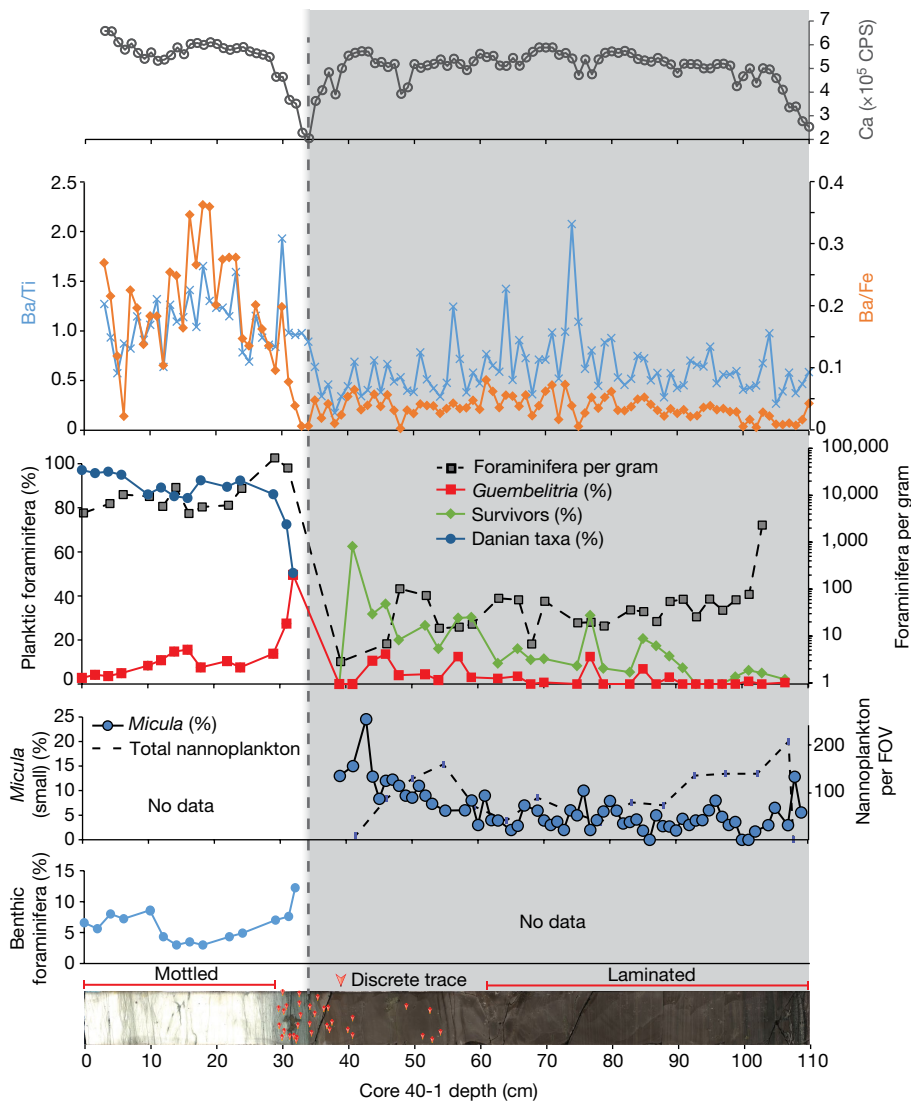


Fig. 1 | Palaeoproductivity indicators in the earliest Palaeocene at site M0077. The shaded area is the transitional unit and the dashed line represents the contact with the overlying pelagic limestone. Top to bottom: X-ray fluorescence-derived calcium abundance in counts per second (CPS); Ba/Ti and Ba/Fe ratios; percentage abundances of key planktic foraminiferal groups, including percentage of *Guembelitrina*, percentage of survivors (that is, Cretaceous species known to survive the impact) and percentage of Danian taxa (that is, species that evolved after the impact)

1 kyr, which is below the resolution of the method. With no sediment source other than settling of material suspended by the impact and subsequent tsunami and seiches, a more realistic estimate—based on

as a percentage of total foraminifera; foraminifera per gram of sediment, plotted on a logarithmic scale; percentage of *Micula* smaller than 2 μm (against total nannoplankton) and nannoplankton abundance (total occurrences per field of view (FOV)); percentage of benthic foraminifera (against total foraminifera); and core image of 364-M0077A-40R-1 0–110 cm (616.58–617.33 m below seafloor), with discrete trace fossils highlighted by arrows (see Extended Data Fig. 2 for a larger version of this image).

Stokes' law—for the duration of this unit suggests about 6 years for the settling of a 2- μm grain of carbonate (an upper limit, as most grains are much larger; see Supplementary Information for further discussion).

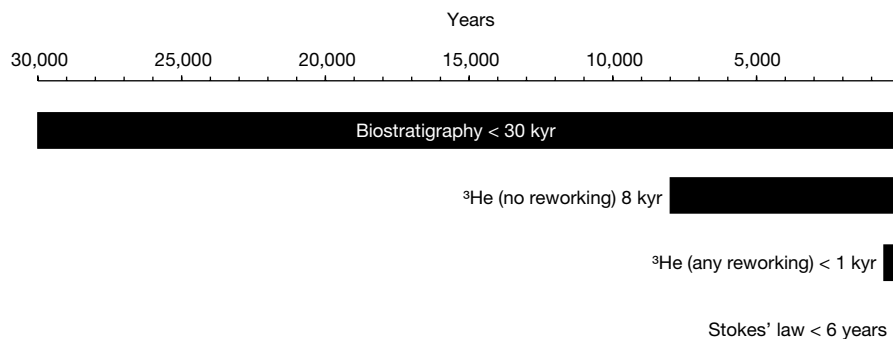


Fig. 2 | Constraints on the age of the transitional unit. Maximum durations of the transitional unit based on biostratigraphy (which suggests it was deposited in less than 30 kyr), extraterrestrial ^3He (which suggests

it was deposited in approximately 8 kyr if there is no reworking, or less than 1 kyr if there is any reworking) and Stokes' law, which suggests it was deposited in less than 6 years.

The lower portion of the overlying limestone, which contains fossils that appear approximately 30 kyr after the impact, appears conformable with the transitional unit and must therefore be condensed owing to low pelagic sedimentation in the first few tens of thousands of years after the impact.

Clear, discrete trace fossils, including *Planolites* and *Chondrites*, characterize the upper 20 cm of the transitional unit (above 54 cm) (Fig. 1 and Extended Data Fig. 2), providing unequivocal evidence for benthic life in the crater within years of the impact. Flattening of the structures indicates that the traces were formed while the sediment was still soft, during or shortly after the deposition of the transitional unit. Infilling of the burrows with brown, fine-grained micrite also suggests traces were syndepositional and not derived from mixing of the Danian limestone above the transitional unit. Trace fossils produced during deposition of the limestone, as indicated by light infilling material, are distinct and occur only in the uppermost few centimetres of the transitional unit (Extended Data Fig. 2).

The transitional unit microfossils are dominated by clearly reworked Maastrichtian foraminifera and nannoplankton, known across the Gulf of Mexico and Caribbean as the Cretaceous/Palaeogene (K/Pg) boundary cocktail¹⁹ (Extended Data Fig. 3 and Supplementary Table 1). Although overall foraminiferal abundance (plotted as the number of foraminifera per gram of sedimentary rock; Fig. 1) is high at the base of the unit, species known to range across the boundary ('survivor species') are rare in the lower transitional unit and become more common up-section even as total foraminifera decline (Fig. 1). Survivor species, here defined as *G. cretacea*, *Muricohedbergella monmouthensis* and *Muricohedbergella holmdelensis*²⁰, dominate a depauperate assemblage in the upper 20 cm of the transitional unit, coinciding with the first appearance of trace fossils (Extended Data Figs. 4, 5).

The nannofossil assemblage in the transitional unit contains reworked Cretaceous specimens, including a group of clearly overgrown species (such as *Aspidolithus parvus* (also known as *Broinsonia parva*) and *Eiffellithus eximius*) that became extinct near the Campanian/Maastrichtian boundary. The remainder of the Cretaceous species, which dominate the assemblage, range to the top of or beyond the latest Maastrichtian age (Supplementary Table 2). Unusually small (less than 2 µm) and delicate specimens of *Micula* are observed throughout the transitional unit and increase in abundance up-section (Fig. 1), along with small *Retecapsa* (Extended Data Fig. 6). Taxa common at other sites of the earliest Danian stage are also present, including disaster genera (opportunistic groups that can tolerate high environmental stress) such as *Thoracosphaera* and *Braarudosphaera*. Unlike the foraminifera, there are no clear stratigraphic trends in overall nannoplankton abundance (Fig. 1).

Because survivor species lived both before and after the K/Pg mass extinction, it is impossible to determine for certain whether individual specimens in the transitional unit colonized the crater after the impact. However, the populations of foraminifera and nannoplankton are substantially different from those of the latest Cretaceous¹² (that is, the expected population if the whole assemblage was reworked), suggesting that these taxa were true survivors (Fig. 1 and Extended Data Fig. 6). *G. cretacea*, a common component of the survivor assemblage in the upper transitional unit, was restricted to marginal marine waters during the Maastrichtian and would not have been present at the pre-impact site, which was over 100 m deep²¹ and over 500 km from shore²². The nannofossil assemblage in the transitional unit is considerably different from typical latest Maastrichtian assemblages, with some genera over-represented (*Watznaueria* and *Retecapsa*) and others under-represented (*Eiffellithus*, not including *E. eximius*, *Arkhangelskiella*, *Chiastozygus* and *Prediscosphaera*) (Extended Data Fig. 6). Additionally, *Micula*—a robust taxon often used as a proxy for dissolution—is not as abundant as elsewhere, indicating that these unusual abundances are not due to poor or selective preservation (Extended Data Fig. 6).

This initial appearance of life is notably fast, especially because crater-specific factors do not seem to have had a negative effect on the

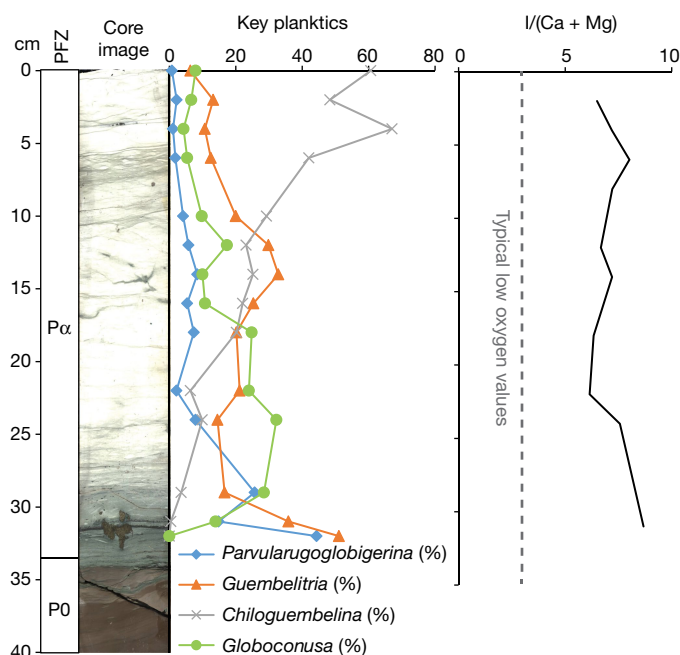


Fig. 3 | Early Danian foraminifer abundances and I/(Ca + Mg) oxygenation proxy. Left plot, Key Danian planktic foraminifera.

Normal perforate planktic foraminifera (*Eoglobigerina*, *Globanomalina*, *Parasubbotina* and *Praemurica*) are rare throughout the study interval and not plotted here; all are plotted as a percentage of total planktic foraminifera. Right plot, I/(Ca + Mg) redox proxy, indicating well-oxygenated conditions in the Chicxulub crater through this interval. PFZ, planktic foraminifer zone.

local recovery of life. A vigorous, high-temperature hydrothermal system was established within the crater and may have persisted for millions of years after the impact²³, especially across the peak ring where rocks exhumed from deep in the crust were extensively fractured⁷. Nevertheless, the appearance of burrowing organisms within years of the impact indicates that the hydrothermal system did not adversely affect seafloor life. Impact-generated hydrothermal systems are hypothesized to be potential habitats for early life on Earth²⁴ and on other planets, particularly below the surface. However, for marine impact craters in open ocean communication, such as Chicxulub (Extended Data Fig. 1), our data indicate that locally substantial but comparatively small volumes of hydrothermal fluids were overwhelmed by the $1.3 \times 10^4 \text{ km}^3$ of well-mixed ocean water that filled the basin.

Likewise, the open connection with the Gulf of Mexico prevented the development of anoxia in the crater. Our analyses of I/Ca ratios suggest that local dissolved oxygen was high and stable in Zone Pα (Fig. 3). This is in contrast to the smaller (85-km wide) Eocene Chesapeake Bay impact crater, where anoxia due to restriction is attributed as the cause of delayed recovery of the benthic ecosystem on the crater floor²⁵. This comparison suggests that the establishment of life within marine impact craters is controlled more by circulation (and thus crater geometry) than by the magnitude of the impact or global environmental effects.

The overlying pelagic limestone, which was deposited within Zone Pα (30–200 kyr after the impact) contains abundant evidence of high productivity in a thriving ecosystem. The assemblage of planktic foraminifera in Zone Pα is diverse and abundant (Fig. 3). Good preservation in the lowermost sample (34 cm core depth) enabled the identification of over 60 species of benthic foraminifera, and benthics make up 12% of the total foraminiferal assemblage at this level (Supplementary Table 1). This percentage of benthics²⁶ and the overall benthic assemblage²⁷ are both typical of a palaeo-water depth of about 600–700 m (around the boundary between the upper and middle bathyal zones)^{10,27}. At the base of the white limestone, trace fossils increase in size, abundance and diversity relative to the underlying

transitional unit. The abundance and diversity of benthic organisms indicate that by about 30 kyr after the impact, seafloor conditions had returned to normal and sufficient organic matter flux existed to sustain a diverse, multilayer benthic community.

Conversely, the nannoplankton assemblage in the Danian limestone is dominated by *Braarudosphaera* and calcareous dinoflagellate cysts (for example, *Thoracosphaera*), which are common disaster taxa in the early recovery interval. Large, foraminifer-sized calcispheres appear after about 100 kyr. Calcareous phytoplankton in the earliest Danian clearly represent a low-diversity, high-productivity bloom. Genera such as *Neobiscutum* and *Prinsius*, which are common bloom taxa in the recovery interval at other Northern Hemisphere sites, do not become common until several metres higher in the section, over one million years after the impact. Organic microfossils are completely absent from the study interval, probably owing to poor preservation of organic material.

Geochemical palaeoproductivity proxies, particularly Ba/Ti and Ba/Fe ratios, also indicate high productivity in the post-impact Danian limestone (Fig. 1). Ba/Ti ratios of about 1.0 at the base of the limestone (approximately 30 kyr after the impact) and about 2.0 above that (15 cm higher, or about 100 kyr after the impact) indicate relatively high and increasing productivity in the Chicxulub basin in the earliest Danian.

The recovery of productivity in the crater is faster than that at many sites, including those in the Gulf of Mexico, some of which took 300 kyr or more to recover to a similar extent^{8,11}. Therefore, we find that proximity to the impact was not a control on recovery in marine ecosystems. The wide range of rates of recovery in the oceans show no relationship with geographic distance to the crater and so are best explained by natural ecological interactions, such as incumbency and competitive exclusion, between organisms within recovery ecosystems^{8,14}. These trends can be used to understand the rates of recovery after other major extinction events and to predict the long-term recovery of modern ecosystems affected by pollution and climate change.

Online content

Any Methods, including any statements of data availability and Nature Research reporting summaries, along with any additional references and Source Data files, are available in the online version of the paper at <https://doi.org/10.1038/s41586-018-0163-6>.

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- Jablonski, D. in *Extinction Rates* (eds Lawton, J. H. & May, R. M.) 25–44 (Oxford Univ. Press, Oxford, 1995).
- Schulte, P. et al. The Chicxulub asteroid impact and mass extinction at the Cretaceous–Paleogene boundary. *Science* **327**, 1214–1218 (2010).
- Alvarez, L. W., Alvarez, W., Asaro, F. & Michel, H. V. Extraterrestrial cause for the Cretaceous–Tertiary extinction. *Science* **208**, 1095–1108 (1980).
- Smit, J. & Hertogen, J. An extraterrestrial event at the Cretaceous–Tertiary boundary. *Nature* **285**, 198–200 (1980).
- Renne, P. R. et al. Time scales of critical events around the Cretaceous–Paleogene boundary. *Science* **339**, 684–687 (2013).
- Hildebrand, A. R. et al. Chicxulub crater: a possible Cretaceous/Tertiary boundary impact crater in the Yucatán Peninsula, Mexico. *Geology* **19**, 867–871 (1991).
- Morgan, J. V. et al. The formation of peak rings in large impact craters. *Science* **354**, 878–882 (2016).
- Hull, P. M. & Norris, R. D. Diverse patterns of ocean export productivity change across the Cretaceous–Paleogene boundary: new insights from biogenic barium. *Paleoceanography* **26**, PA3205 (2011).
- Alegret, L. & Thomas, E. Cretaceous/Paleogene boundary bathyal paleo-environments in the central North Pacific (DSDP site 465), the northwestern Atlantic (ODP site 1049), the Gulf of Mexico, and the Tethys: the benthic foraminiferal record. *Palaeogeogr. Palaeoclimatol. Palaeoecol.* **224**, 53–82 (2005).
- Alegret, L., Molina, E. & Thomas, E. Benthic foraminifera at the Cretaceous–Tertiary boundary around the Gulf of Mexico. *Geology* **29**, 891–894 (2001).
- Alegret, L., Arenillas, I., Arz, J. A. & Molina, E. Foraminiferal event-stratigraphy across the Cretaceous/Paleogene boundary. *Neues Jahrb. Geol. Paläontol. Abh.* **231**, 25–50 (2004).

- Jiang, S., Bralower, T. J., Patzkowsky, M. E., Kump, L. R. & Schueth, J. D. Geographic controls on nannoplankton extinction across the Cretaceous/Paleogene boundary. *Nat. Geosci.* **3**, 280–285 (2010).
- Solé, R. V., Montoya, J. M. & Erwin, D. H. Recovery after mass extinction: evolutionary assembly in large-scale biosphere dynamics. *Philos. Trans. R. Soc. Lond. B* **357**, 697–707 (2002).
- Schueth, J. D., Bralower, T. J., Jiang, S. & Patzkowsky, M. E. The role of regional survivor incumbency in the evolutionary recovery of calcareous nannoplankton from the Cretaceous/Paleogene (K/Pg) mass extinction. *Paleobiology* **41**, 661–679 (2015).
- Hull, P. M., Norris, R. D., Bralower, T. J. & Schueth, J. D. A role for chance in marine recovery from the end-Cretaceous extinction. *Nat. Geosci.* **4**, 856–860 (2011).
- Yedid, G., Ofria, C. A. & Lenski, R. E. Selective press extinctions, but not random pulse extinctions, cause delayed ecological recovery in communities of digital organisms. *Am. Nat.* **173**, E139–E154 (2009).
- Gulick, S., Morgan, J., Mellett, C. L. & the Expedition 364 Scientists. *Expedition 364 Preliminary Report: Chicxulub: Drilling the K-Pg Impact Crater* (International Ocean Discovery Program, College Station, TX, 2017).
- Wade, B. S., Pearson, P. N., Berggren, W. A. & Pälike, H. Review and revision of Cenozoic tropical planktonic foraminiferal biostratigraphy and calibration to the geomagnetic polarity and astronomical time scale. *Earth Sci. Rev.* **104**, 111–142 (2011).
- Bralower, T. J., Paull, C. K. & Leckie, R. M. The Cretaceous–Tertiary boundary cocktail: Chicxulub impact triggers margin collapse and extensive sediment gravity flows. *Geology* **26**, 331–334 (1998).
- Olsson, D. K., Hemleben, C., Berggren, W. A. & Huber, B. T. *Atlas of Paleocene Planktonic Foraminifera* (Smithsonian Institution, Washington, 1999).
- Gulick, S. P. S. et al. Importance of pre-impact crustal structure for the asymmetry of the Chicxulub impact crater. *Nat. Geosci.* **1**, 131–135 (2008).
- Sohl, N. F., Martínez, E. R., Salmerón-Ureña, P. & Soto-Jaramillo, F. in *Geology of North America, Volume J: Gulf of Mexico Basin* (ed. Salvador, A.) 205–244 (Geological Society of America, Boulder, 1991).
- Abramov, O. & Kring, D. A. Numerical modeling of impact-induced hydrothermal activity at the Chicxulub crater. *Meteorit. Planet. Sci.* **42**, 93–112 (2007).
- Cockell, C. S. The origin and emergence of life under impact bombardment. *Phil. Trans. R. Soc. Lond. B* **361**, 1845–1856 (2006).
- Poag, C. W. in *The ICDP-USGS Deep Drilling Project in the Chesapeake Bay Impact Structure: Results from the Eyreville Core Holes* (The Geological Society of America Special Paper 458) (eds Gohn, G. S. et al.) 747–773 (Geological Society of America, Boulder, 2009).
- Leckie, R. M. & Olson, H. C. In *Micropaleontologic Proxies for Sea-level Change and Stratigraphic Discontinuities* (SEPM Special Publication 75) (eds Olson, H. C. & Leckie, R. M.) 5–19 (Society for Sedimentary Geology, Tulsa, 2003).
- Alegret, L. & Thomas, E. Upper Cretaceous and lower Paleocene benthic foraminifera from northeastern Mexico. *Micropaleontology* **47**, 269–316 (2001).

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Competing interests The authors declare no competing interests.

Additional information

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METHODS

Sample size was determined according to standard community practice (collecting approximately 300 specimens per sample, when possible). No statistical methods were used to predetermine sample size. The experiments were not randomized and investigators were not blinded to allocation during experiments and outcome assessment.

The IODP–ICDP Expedition 364 drilled the peak ring of the Chicxulub crater in the spring of 2016 (Extended Data Fig. 1). Samples were taken at the Bremen IODP core repository during the Expedition 364 sampling party. Core depth in centimetres—with zero at the top of the section (616.24 m below sea floor)—are reported throughout. Core material was indurated, and ~0.5-cm quarter-rounds were cut out with a rock saw. Owing to the need to reserve core material for rare earth element geochemistry (data not shown), the lowermost ~1.5 cm of the Danian limestone was not sampled. Individual samples were subdivided for foraminifera, calcareous nannoplankton and discrete geochemical analyses.

Forty-three samples were examined for planktic and benthic foraminifera from core 40 from 0–110 cm depth. Samples were weighed, crushed with a mortar and pestle, soaked overnight (or longer) in a 10% solution of hydrogen peroxide buffered with borax and washed over a 43- μ m sieve to ensure capture of small Danian taxa. The sieve was soaked in methylene blue dye between samples to identify contaminated specimens. Samples were then dried in an oven, split to obtain a manageable volume of material, and examined for foraminifera, calcispheres, and other sand-sized particles. In the Danian limestone, at least 300 specimens were counted to establish a statistically robust population²⁸ and the rest of the residue was then examined for biostratigraphically important taxa. Low abundances in the transitional unit precluded 300-specimen counts. However, we demonstrate that our values are sufficient to reject the null hypothesis (that the observed enrichments in survivor taxa are the result of random noise) with binomial confidence limits. This calculation traditionally provides the basis for the 300-specimen ‘rule’: counting 300 specimens provides statistical confidence at a 95% confidence interval that a species that makes up 1% of the population is represented in the count²⁸. As we show, fewer specimens are sufficient to demonstrate the presence of a survivor population in our samples. Binomial confidence limits for samples with fewer than 300 specimens are reported in Supplementary Table 1. Additionally, a single unusually well-preserved sample at the base of the post-impact limestone was examined for rare benthic species to determine the true diversity of benthic foraminifera at the base of the unit (Supplementary Table 1). Planktic foraminifer biozonation follows the P zones of Berggren and Pearson²⁹ as modified by Wade et al.¹⁸.

Ninety-seven samples were examined for nannofossils. Samples were disaggregated in water, and smear slides were made from the supernatant. Slides were observed in a transmitted light microscope at 1,600 $\times$ until at least 100 specimens were observed (Supplementary Table 2). Standard taxonomy was applied (<http://www.mikrotax.org/Nannotax3/index.php?dir=Coccolithophores>). The abundance of taxa at site M0077 was compared to a previous compilation of global K/Pg nannoplankton¹².

Ichnological analysis was conducted from 0–110 cm. Ichnological observations were conducted on core material and a detailed and continuous analysis of digital images. To improve visibility of ichnological features, images were treated by a digital image methodology, based on the modification of image adjustments as levels, brightness and vibrance^{30,31}. Ichnotaxonomical classification of trace fossils was based on the overall shape and the presence of diagnostic criteria such as size and presence of branches³². Special attention was given to the infilling material of biogenic structures.

The measurement of I/(Ca + Mg) was carried out using a procedure similar to a previously described method³³. For each sample and geostandard, approximately 3–4 mg of carbonate powder was weighed out, dissolved in ~0.45 M nitric solution and then diluted using 0.1 M nitric acid and 0.5% TMAH solution. All reported measurements are from samples that had a matrix of 50 ± 5 p.p.m. calcium solution to ensure the most precise iodine measurement. Dissolved samples had TMAH solution added within an hour to avoid any possible loss of volatilized iodine³³. Samples were measured using an Agilent inductively coupled plasma mass spectrometer 7500 cs housed within the geochemistry group of the National High Magnetic Field Laboratory at Florida State University. A previously reported known sample, Key Largo (KL 1-1) was used to ensure reliable reproducibility. Our value of 5.51 μ mol/mol was within error of the reported value of 5.55 μ mol/mol. A previous study³⁴ found that generally low oxygen conditions correspond to ~2.6 μ mol/mol for I/(Ca + Mg). Values are reported in Supplementary Table 3.

Section 1 of core 40 was scanned with an AVAATECH XRF Core Scanner II at MARUM (Bremen, Germany) during the onshore phase of Expedition 364 (Fig. 1). The split core was covered with a 4- μ m-thick SPEX CertiPrep Ultralene foil to avoid contamination. X-ray fluorescence data were acquired with a Canberra X-PIPS silicon drift detector with 1550 eV resolution, a Canberra DAS 1000 dig-

ital spectrum analyser and an Oxford Instruments 50 W XTF011 X-ray tube with rhodium target material. X-ray spectra were processed with WIN AXIL software from Canberra Erisys at a resolution of 12 mm and a step of 10 mm. Scans were conducted at different voltages to determine a range of element concentrations: 50 kV, with a beam current of 1 mA (Ba and Sr; average dead time of 5%), and 10 kV with a beam current of 0.15 mA (Al, Si, K, Ca, Ti, Fe, Mn and S; average dead time of 11%). For each scan, sampling time was 20 s per spot.

³He is delivered to the Earth's surface by cosmic dust grains and over short time spans (about one million years) can be used as a constant flux proxy³⁵. Previous work has shown that the K/Pg impactor was not associated with enhanced ³He flux, and the mean extraterrestrial ³He flux from cosmic dust accretion at the end of the Cretaceous (106×10^{-15} cc (standard temperature and pressure) per g per cm² per kyr) was used to estimate the duration over which the K/Pg boundary clay was deposited at Gubbio and El Kef³⁶. We use a similar approach here to establish the sedimentation rate of the transitional unit, which we use to develop an age model.

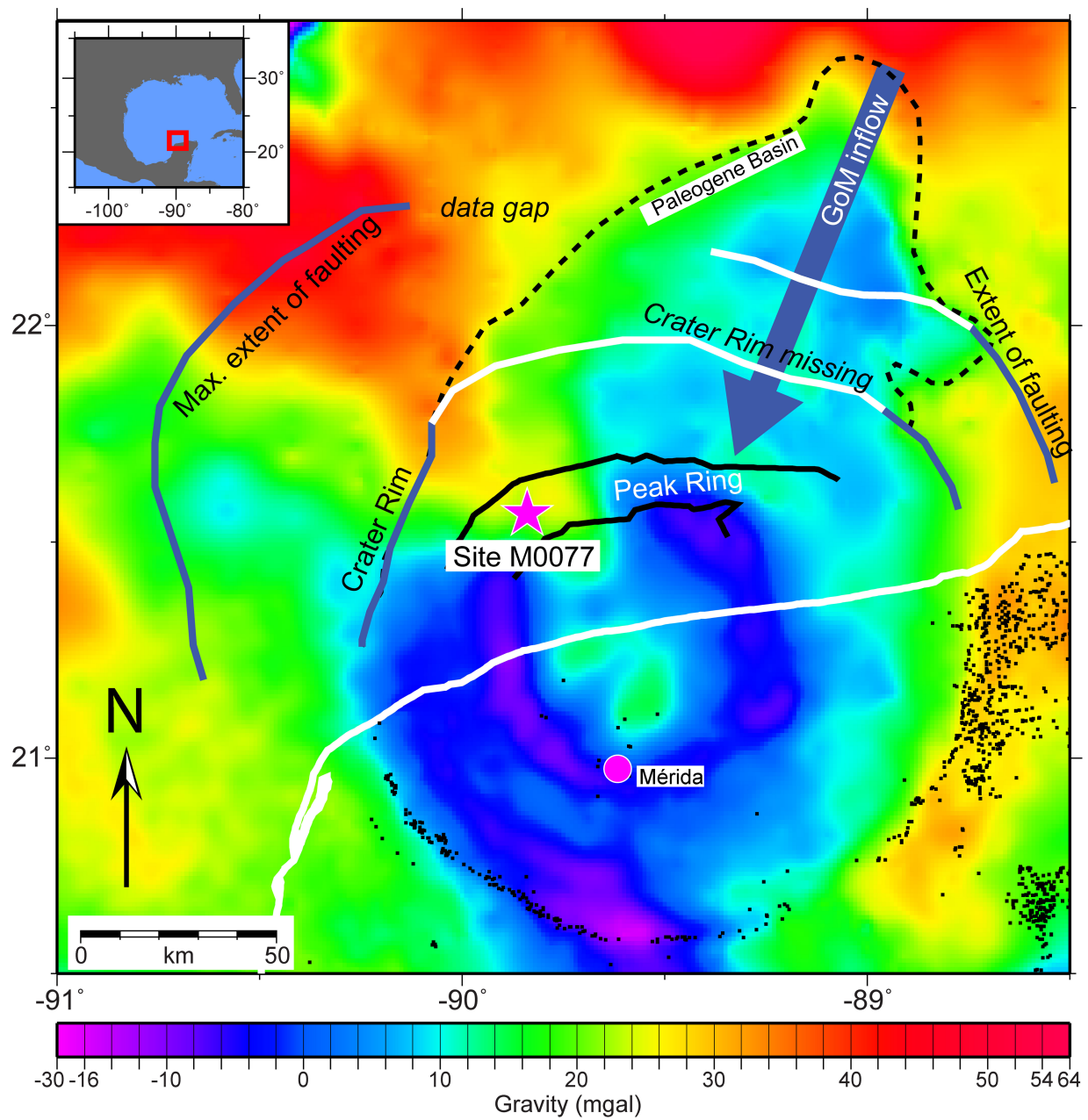
Helium isotope ratios and concentrations were measured on ~1-g aliquots of sediment following standard analytical procedures³¹. Extraterrestrial ³He concentrations were computed from measured He isotopic compositions using an isotopic deconvolution model³⁶. Results are shown in Extended Data Table 1. ³He concentrations and ³He/⁴He ratios are generally low compared to typical marine sediments of similar age^{37,38}. Nevertheless, with the exception of the lowest sample in the transitional unit (106.5 cm), the fraction of ³He attributable to an extraterrestrial source is high, ranging from ~0.70 to 0.96. The deepest sample has a similar ³He concentration to other samples in the transitional unit, but ~5 times more ⁴He. This elevated ⁴He probably arises from a higher concentration of terrigenous ⁴He-bearing material deposited rapidly after the impact.

We see no evidence for extraterrestrial He carried in impactor fragments, such as highly elevated and/or highly variable ³He and ³He/⁴He ratios. The absence of such a signal is consistent with either (a) the absence of impactor fragments in the material analysed or (b) the loss of extraterrestrial ³He from the impactor via heating, vaporization or fusion. Note that, unlike many tracers of the impactor (such as Ir), deposition of fused or vaporized impactor will leave no trace in the sedimentary record because once He is lost into the atmosphere, it can no longer be retained in sediments.

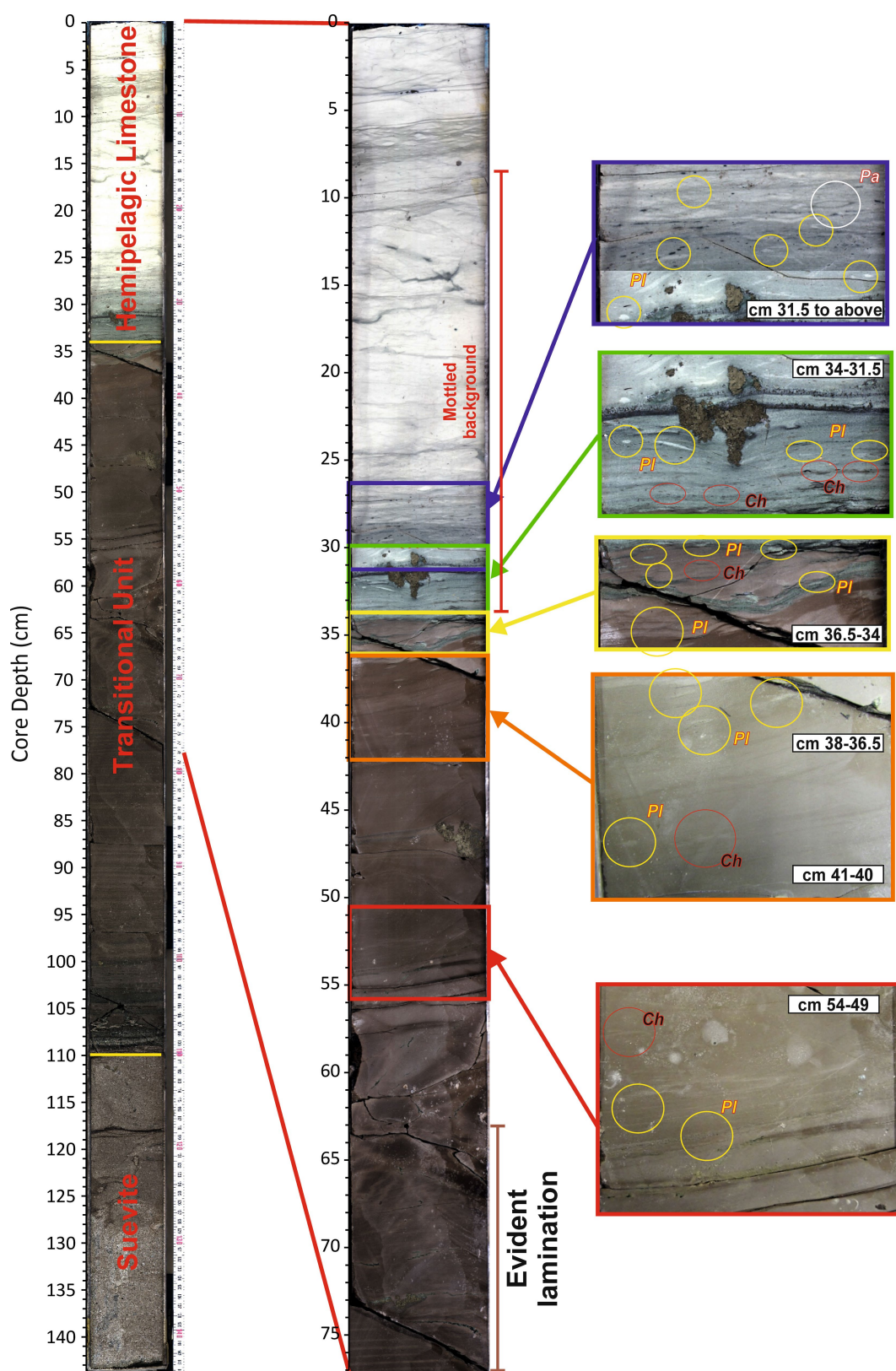
Reporting summary. Further information on experimental design is available in the Nature Research Reporting Summary linked to this paper.

Data availability. X-ray fluorescence data have previously been published³⁹ and are available online (<https://doi.org/10.14379/iodp.proc.364.2017>). All other data supporting the findings of this study are available within the paper and its Supplementary Information.

28. Buzas, M. A. Another look at confidence limits for species proportions. *J. Paleontol.* **64**, 842–843 (1990).
29. Berggren, W. A. & Pearson, P. N. A revised tropical and subtropical Paleogene planktonic foraminiferal zonation. *J. Foraminiferal Res.* **35**, 279–298 (2005).
30. Dorador, J. & Rodríguez-Tovar, F. Digital image treatment applied to ichnological analysis of marine core sediments. *Facies* **60**, 39–44 (2014).
31. Dorador, J. & Rodríguez-Tovar, F. J. Stratigraphic variation in ichnofabrics at the “Shackleton Site” (IODP Site U1385) on the Iberian Margin: paleoenvironmental implications. *Mar. Geol.* **377**, 118–126 (2016).
32. Knaust, D. *Atlas of Trace Fossils in Well Core: Appearance, Taxonomy and Interpretation* (Springer, New York, 2017).
33. Lu, Z., Jenkyns, H. C. & Rickaby, R. E. M. Iodine to calcium ratios in marine carbonate as a paleo-redox proxy during oceanic anoxic events. *Geology* **38**, 1107–1110 (2010).
34. Hardisty, D. S. et al. Perspectives on Proterozoic surface ocean redox from iodine contents in ancient and recent carbonate. *Earth Planet. Sci. Lett.* **463**, 159–170 (2017).
35. Farley, K. A. & Eltgroth, S. F. An alternative age model for the Paleocene–Eocene thermal maximum using extraterrestrial ³He. *Earth Planet. Sci. Lett.* **208**, 135–148 (2003).
36. Patterson, D. B. & Farley, K. A. Extraterrestrial ³He in seafloor sediments: evidence for correlated 100 kyr periodicity in the accretion rate of interplanetary dust, orbital parameters, and Quaternary climate. *Geochim. Cosmochim. Acta* **62**, 3669–3682 (1998).
37. Mukhopadhyay, S., Farley, K. A. & Montanari, A. A 35 Myr record of helium in pelagic limestones from Italy: implications for interplanetary dust accretion from the early Maastrichtian to the middle Eocene. *Geochim. Cosmochim. Acta* **65**, 653–669 (2001).
38. Mukhopadhyay, S., Farley, K. A. & Montanari, A. A short duration of the Cretaceous–Tertiary boundary event: evidence from extraterrestrial helium-3. *Science* **291**, 1952–1955 (2001).
39. Morgan, J., Gulick, S., Mellet, C. L., Green, S. L. & Expedition 364 Scientists. *Chicxulub: Drilling the K-Pg Impact Crater. Proceedings of the International Ocean Discovery Program 364* (International Ocean Discovery Program, College Station, 2017).

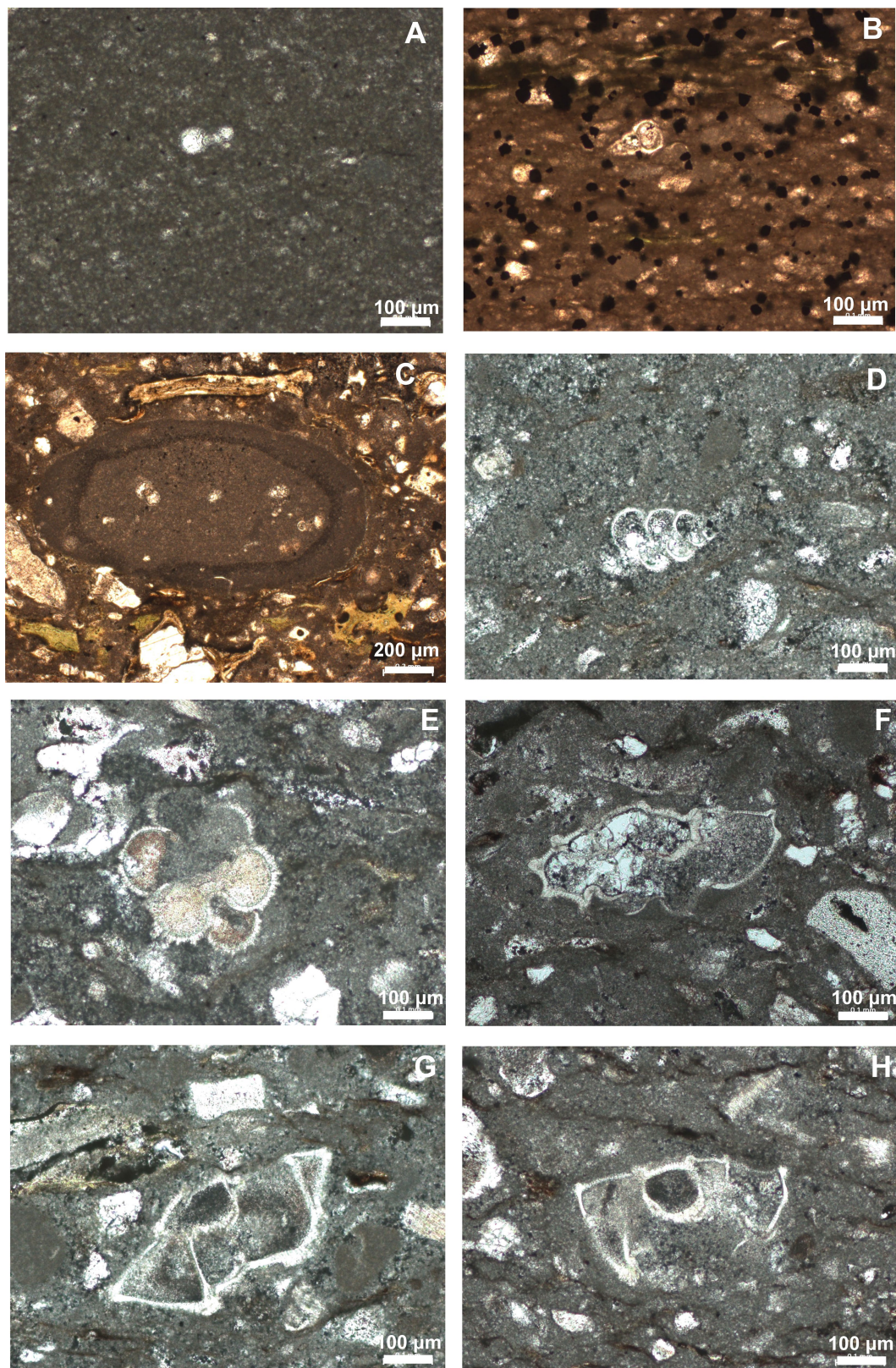


Extended Data Fig. 1 | Location of site M0077 in the Chicxulub crater as seen using gravity data. Black dots are cenotes. Modified from Gulick et al.²¹.



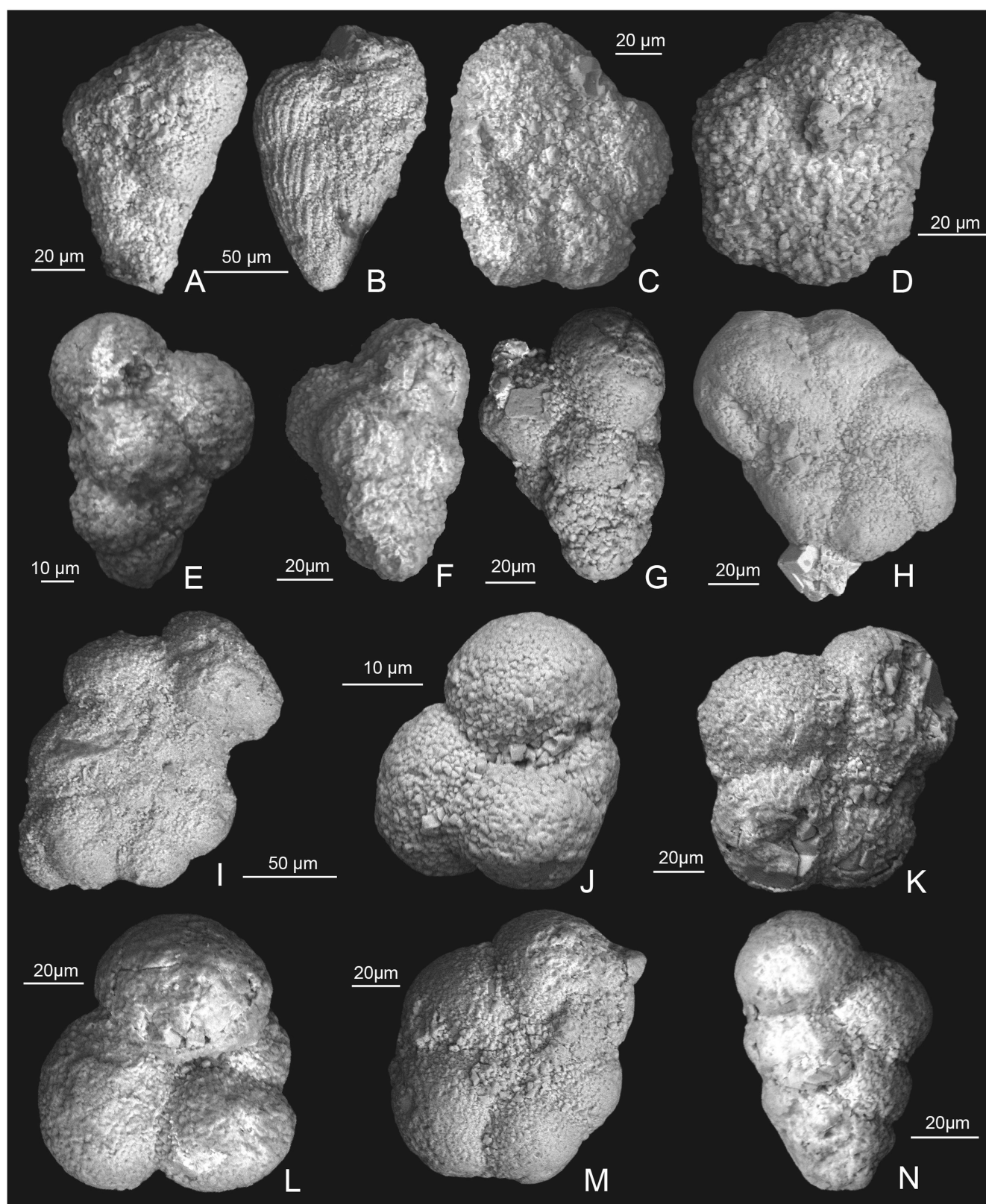
Extended Data Fig. 2 | Trace fossils in core 40 section 1 of IODP hole M0077A. Discrete burrows in the upper transitional unit and the lower limestone are circled and labelled by the genus. Above the base

of the limestone, trace fossils are abundant; representative examples are highlighted in the lower 10 cm of this interval. Ch, *Chondrites*; Pl, *Planolites*; Pa, *Palaeophycus*.



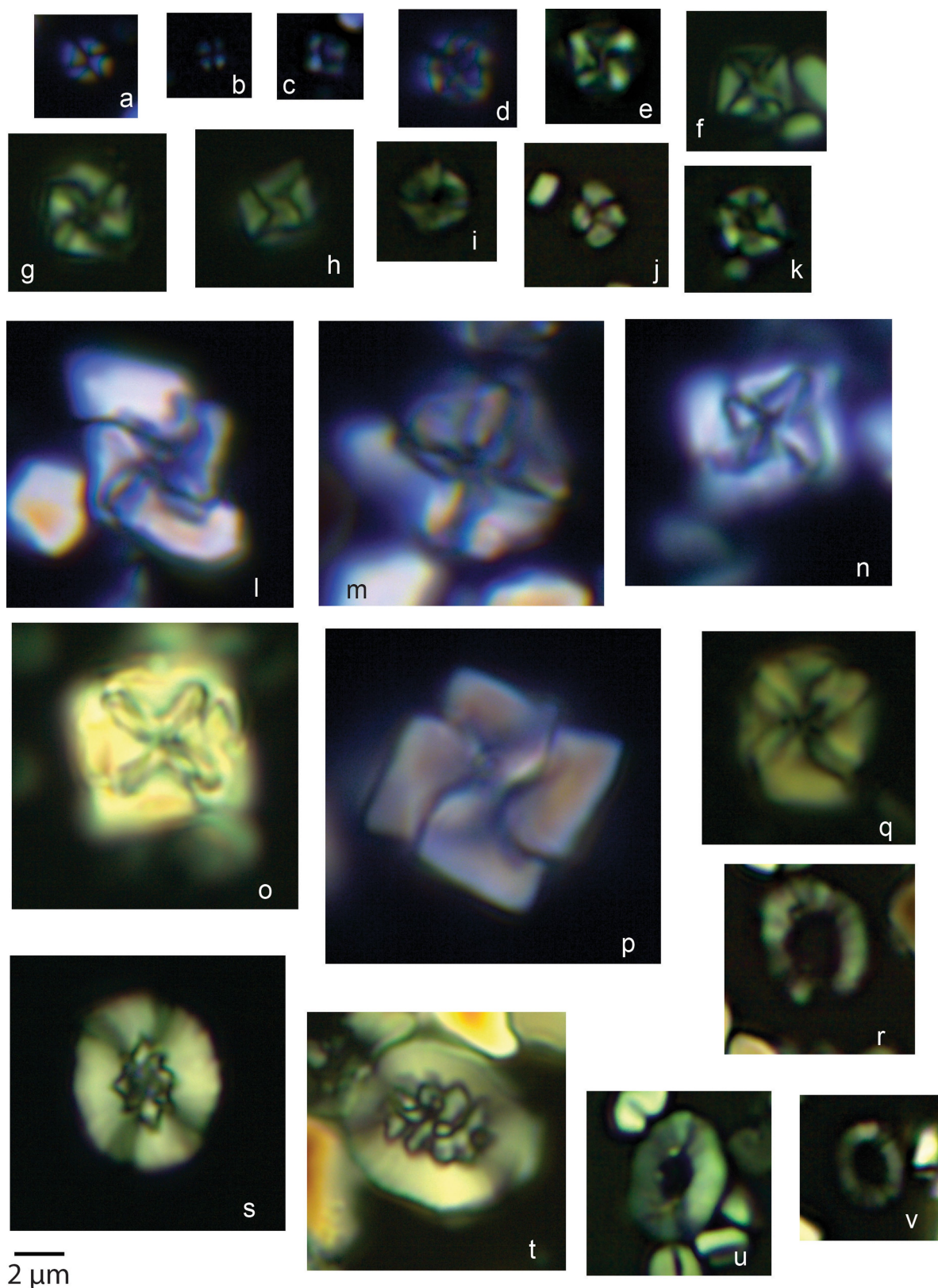
Extended Data Fig. 3 | Reworked Cretaceous foraminifera in the transitional unit. **a**, *Globigerinelloides* sp., sample 364-M0077A-40R-1-W, 55–56 cm. **b**, *Heterohelix* sp., sample 364-M0077A-40R-1-W, 104–105 cm. **c**, Clast of pelagic limestone containing older Cretaceous planktic foraminifera, sample 364-M0077A-40R-1-W, 106–110 cm. **d**, *Praegublerina pseudotessera*, sample 364-M0077A-40R-1-W, 118–129 cm.

e, *Racemiguembelina powelli*, sample 364-M0077A-40R-1-W, 118–129 cm. **f**, *Globotruncana bulloides*, sample 364-M0077A-40R-1-W, 110–118 cm. **g**, *Globotruncanita stuartiformis*, sample 364-M0077A-40R-1-W, 118–129 cm. **h**, *Globotruncanita elevata*, sample 364-M0077A-40R-1-W, 118–129 cm. Scale bars, 100 μm.



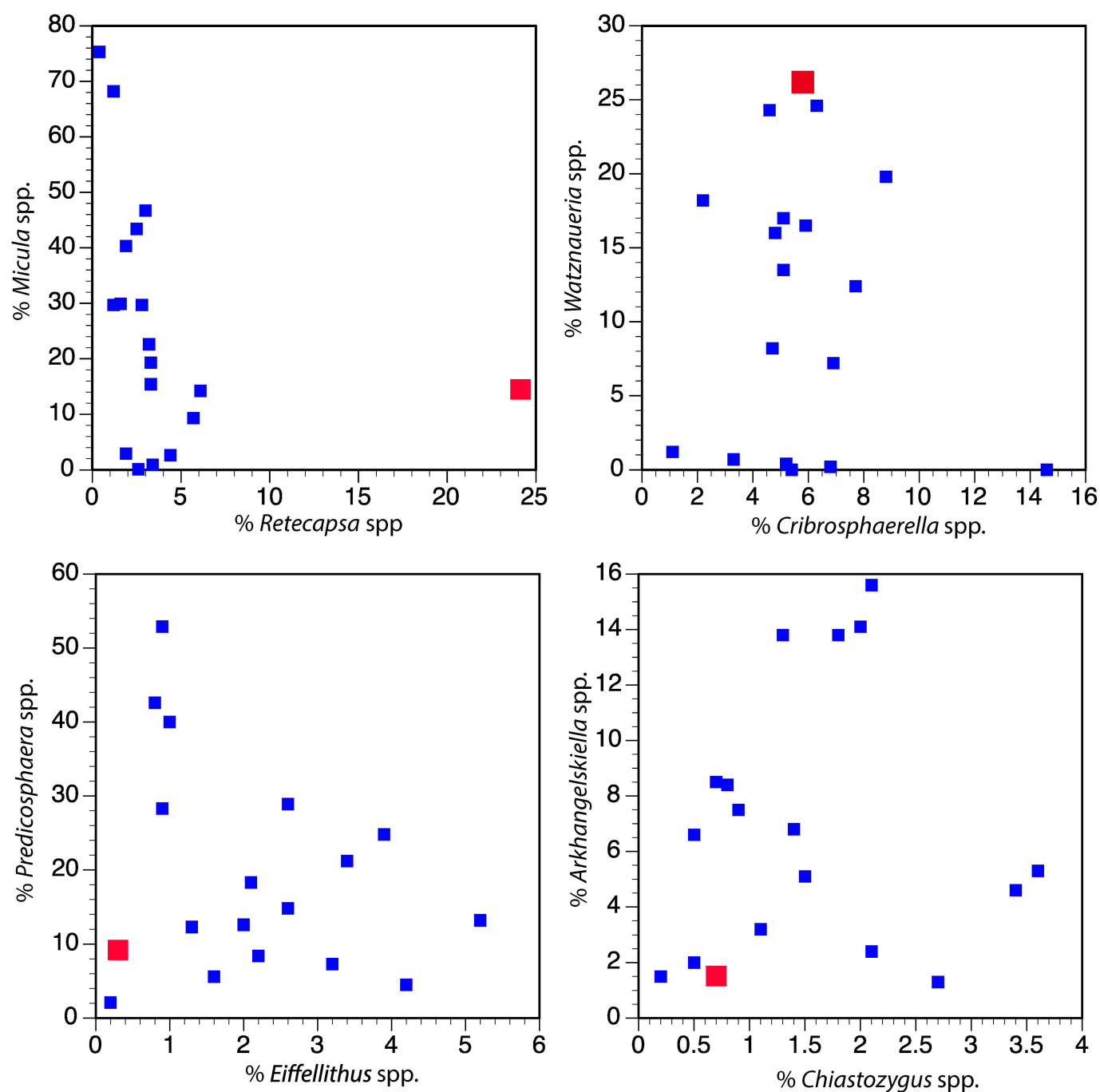
Extended Data Fig. 4 | Scanning electron micrographs of planktic foraminifera from core 40. **a, b**, Examples of common reworked Cretaceous biserials, sample 364-M0077A-40R-1, 102–103 cm. **c**, *Muricohedbergella monmouthensis*, sample 364-M0077A-40R-1-W, 102–103 cm. **d**, *Muricohedbergella holmdelensis*, sample 364-M0077A-40R-1-W, 44–45 cm. **e**, *Guembelitra cretacea*, sample 364-M0077A-40R-1-W, 44–45 cm. **f**, *G. cretacea*, sample 364-M0077A-40R-1-W, 29–30 cm. **g**, *G. cretacea*, sample 364-M0077A-40R-1-W, 29–30 cm. **h**,

Parvularugoglobigerina eugubina 364-M0077A-40R-1-W, 31–32 cm. **i**, *P. eugubina*, sample 364-M0077A-40R-1-W, 31–32 cm. **j**, *Globoconusa daubjergensis*, sample 364-M0077A-40R-1-W, 31–32 cm. **k**, *Eoglobigerina eobulloides*, sample 364-M0077A-40R-1-W, 29–30 cm. **l**, *Eoglobigerina edita*, sample 364-M0077A-40R-1-W, 29–30 cm. **m**, *Praemurica taurica*, sample 364-M0077A-40R-1-W, 10–11 cm. **n**, *Chiloguembelina morsei*, sample 364-M0077A-40R-1-W, 10–11 cm.



Extended Data Fig. 5 | Small and regular-sized nannofossils in the transitional unit. All photographs from core 364-M0077-40R-1-W. Measurements in centimetres refer to depth in section 1 of core 40. **a–k**, Images of small *Micula* spp.: **a**, 55–56 cm; **b**, 41–42 cm; **c**, 95–96 cm; **d**, 41–42 cm; **e**, 90–91 cm; **f**, 94–95 cm; **g**, 91–92 cm; **h**, 91–92 cm; **i**, 45–46 cm;

j, 100–101 cm; **k**, 81–82 cm. **l–q**, Images of regular-sized *Micula* spp.: **l**, 44–45 cm; **m**, 41–42 cm; **n**, 51–52 cm; **o**, 105–106 cm; **p**, 97–98 cm; **q**, 36–37 cm. **s, t**, Images of regular-sized *Retecapsa* spp.: **s**, 85–86 cm; **t**, 100–101 cm. **r–v**, Images of small *Retecapsa* spp.: **r**, 100–101 cm; **u**, 71–72 cm, **v**, 100–101 cm. Scale bar, 2 μ m.



Extended Data Fig. 6 | Relative abundances of major Maastrichtian calcareous nannoplankton. Small blue squares are Maastrichtian sites from a global compilation¹²; larger red squares are from the transitional

unit at site M0077. These data demonstrate the unusual abundance of *Watznaueria* and *Retecapsa* at site M0077.

Extended Data Table 1 | ^3He data

	start	stop	^3He	^4He	Absolute	Fraction	Maximum ^3He -Based
Sample	cm	cm	pcc/g	ncc/g	$^3\text{He}/^4\text{He}$	^3He ET	Model Age (kyr)
KT39	39	40	0.0068	13.6	5.04E-07	0.96	6.0
KT48	48	49	0.0055	35.4	1.56E-07	0.87	4.9
KT59	59	60	0.0064	23.1	2.78E-07	0.92	4.0
KT68	68	69	0.0042	31.6	1.33E-07	0.84	2.9
KT79	79	80	0.0036	18.3	1.99E-07	0.9	1.9
KT89	89	90	0.0105	34.7	3.04E-07	0.93	0.9
KT99	99	100	0.0045	64.3	6.99E-08	0.70	0.1
KT106.5	107	108	0.0109	327	3.32E-08	0.37	0.0

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► Experimental design

1. Sample size

Describe how sample size was determined.

Sample size was determined using standard population sizes for micropaleontological datasets (e.g., Buzas, 1990, J. of Paleo) except for samples which contained fewer than 300 specimens. These were all in the transitional unit, and were only analyzed for the proportion of 2 overall groups (survivors vs. non survivors; Guembeltria vs. everything else) and thus did not require the 300 specimen count needed for more advanced ecological analysis. We show this by reporting binomial confidence intervals for these data in Tables S2 and S3

2. Data exclusions

Describe any data exclusions.

We did not include benthic foraminifera in the %survivors foraminifer dataset (i.e., it is only %planktic survivors out of the total population of planktic foraminifera). Benthics did not experience an extinction at the KPg boundary, so *all* benthics are technically survivors and we felt this would bias the data.

3. Replication

Describe whether the experimental findings were reliably reproduced.

It is hard to judge the reproducibility of paleontological samples, as the act of picking foraminifera from sample changes the remaining population. However, we had several replicate samples from the same depth interval, and these produced very similar proportions of the groups measured (e.g., %benthics, % Parvularugoglobigerina, %Chilguembelina, etc.). Analytical runs for geochemical samples included standards of known composition to constrain error and ensure reproducibility. (see discussion in Methods section).

4. Randomization

Describe how samples/organisms/participants were allocated into experimental groups.

Samples were taken at a regular interval throughout the core. Foraminifer samples were split with a microsplitter to obtain a representative subsample for population counts (when the population was >300); nannoplankton were counted in fields of view along a complete transect.

5. Blinding

Describe whether the investigators were blinded to group allocation during data collection and/or analysis.

No blinding was utilized in this paleoecological/geochemical study.

Note: all studies involving animals and/or human research participants must disclose whether blinding and randomization were used.

6. Statistical parameters

For all figures and tables that use statistical methods, confirm that the following items are present in relevant figure legends (or in the Methods section if additional space is needed).

n/a Confirmed

- ☐ ☒ The exact sample size (n) for each experimental group/condition, given as a discrete number and unit of measurement (animals, litters, cultures, etc.)
- ☐ ☒ A description of how samples were collected, noting whether measurements were taken from distinct samples or whether the same sample was measured repeatedly
- ☒ ☐ A statement indicating how many times each experiment was replicated
- ☐ ☒ The statistical test(s) used and whether they are one- or two-sided (note: only common tests should be described solely by name; more complex techniques should be described in the Methods section)
- ☒ ☐ A description of any assumptions or corrections, such as an adjustment for multiple comparisons
- ☐ ☒ The test results (e.g. P values) given as exact values whenever possible and with confidence intervals noted
- ☒ ☐ A clear description of statistics including central tendency (e.g. median, mean) and variation (e.g. standard deviation, interquartile range)
- ☒ ☐ Clearly defined error bars

See the web collection on [statistics for biologists](#) for further resources and guidance.

► Software

Policy information about [availability of computer code](#)

7. Software

Describe the software used to analyze the data in this study.

Data were input and plotted in Excel.

For manuscripts utilizing custom algorithms or software that are central to the paper but not yet described in the published literature, software must be made available to editors and reviewers upon request. We strongly encourage code deposition in a community repository (e.g. GitHub). *Nature Methods* [guidance for providing algorithms and software for publication](#) provides further information on this topic.

► Materials and reagents

Policy information about [availability of materials](#)

8. Materials availability

Indicate whether there are restrictions on availability of unique materials or if these materials are only available for distribution by a for-profit company.

Our own sample materials will be available by request; additional core material from Exp. 364 will be housed at the IODP Gulf Coast Repository in College Station, TX and will be available for sampling.

9. Antibodies

Describe the antibodies used and how they were validated for use in the system under study (i.e. assay and species).

N/A

10. Eukaryotic cell lines

a. State the source of each eukaryotic cell line used.

N/A

b. Describe the method of cell line authentication used.

N/A

c. Report whether the cell lines were tested for mycoplasma contamination.

N/A

d. If any of the cell lines used are listed in the database of commonly misidentified cell lines maintained by [ICLAC](#), provide a scientific rationale for their use.

N/A

► Animals and human research participants

Policy information about [studies involving animals](#); when reporting animal research, follow the [ARRIVE guidelines](#)

11. Description of research animals

Provide details on animals and/or animal-derived materials used in the study.

N/A

12. Description of human research participants

Describe the covariate-relevant population characteristics of the human research participants.

N/A