Title: Global record of 'ghost' nannofossils reveals plankton resilience to high-CO_2 and warming

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Abstract: Predictions of how marine calcifying organisms will respond to climate change rely heavily on the fossil record of nannoplankton. Declines in nannofossil abundance and calcium carbonate ($CaCO_3$) through several past global warming events have been interpreted as 'biocalcification crises' caused by ocean acidification and related factors. We present a global record of imprint, or 'ghost', nannofossils that oppose this view, revealing exquisitely preserved nannoplankton throughout an inferred Jurassic biocalcification crisis. Imprints from two further Cretaceous warming events confirm that the fossil records of these intervals have been strongly distorted by $CaCO_3$ dissolution. Although the rapidity of current climate change exceeds the

temporal resolution of most fossil records, making direct comparison with past warming events challenging, our findings demonstrate that nannoplankton were more resilient to past events than traditional fossil evidence would suggest.

One-Sentence Summary: Discovery of plankton imprint fossils challenges inferred links between past global warming events and biocalcification crises.

Main Text: As CO_2-levels in the atmosphere rise, resultant ocean acidification (OA) and declining seawater carbonate ion concentrations will likely make it more difficult for marine organisms to form their calcium carbonate ($CaCO_3$) skeletons or shells (*1*, *2*). Coccolithophores, a group of unicellular phytoplanktonic algae (also known as nannoplankton), are the most productive marine calcifiers (*3*), but predicting their response to future environmental change has proved challenging. Experiments testing the effects of high-CO_2 and temperatures on living coccolithophores and their calcitic exoskeletons have shown apparently contradictory results within and between species (*4*–*8*). However, interpretations of geological and fossil-based evidence have evoked globally catastrophic responses in nannoplankton during past intervals of high temperature and CO_2 (reviewed in Data S1 to S3). Specifically, prominent studies have observed major declines in $CaCO_3$ and nannoplankton abundance through past global warming events, and interpreted these signals as 'biocalcification crises', whereby OA, and related environmental change, directly compromised biogenic $CaCO_3$ production. Contrary to this, others have argued that these declines in $CaCO_3$ are caused by dissolution of carbonate at the seafloor during these events, and that independent evidence for nannoplankton responses to OA needs to be better understood and demonstrated before biocalcification crises are invoked (*9*, *10*). However, the biocalcification crisis paradigm continues to be widely applied to past warming episodes, especially the Mesozoic oceanic anoxic events (OAEs; Data S1 to S3), and given that this model predicts potentially disastrous changes to future marine biodiversity and carbon cycle function, we tested this hypothesis using a novel methodology.

We examined one of the most severe reported biocalcification crises of the last 200 million years, associated with the Toarcian Oceanic Anoxic Event (T-OAE; ~183 million years ago [Ma]) in the Early Jurassic. The T-OAE was a geologically-rapid global warming event caused by volcanism in the Southern Hemisphere (*11*), and is characterized by a range of environmental,

geological and ecological changes, including high-CO_2, OA, oceanic anoxia, the deposition of organic-rich sediments, a major negative carbon isotope excursion, and widespread extinction (*12* and references therein). Previous interpretations of the biocalcification crisis are primarily based on declining $CaCO_3$ in the sedimentary rock record and decreased nannoplankton species abundances and sizes (Data S1), but crucially this evidence has relied upon conventional nannofossil analyses, whereby data are derived from calcite 'body' fossils. Here we report on an overlooked form of preservation, namely imprint, or 'ghost' nannofossils, which provides critical information that may be lost from the more routinely studied 'body' fossil record.

Toarcian rock samples from the UK, Germany, Japan and New Zealand (Fig. S1) were processed for organic matter analysis. Scanning electron microscopy (SEM) of organic particles revealed nannoplankton imprints preserved on the surfaces of marine organic-walled plankton (dinoflagellate cysts, prasinophytes and acritarchs), amorphous organic matter (AOM), and spores and pollen from land plants (Fig. 1). Imprints are also visible using transmitted-light, fluorescence, and confocal microscopy (Fig. S2), but exquisite details are evident using SEM, with specimens displaying diagnostic coccolith rims, radial and imbricating sutures, and fragile axial and radiating central structures (Figs. S3 to S12). Preservation is often pristine, and digital inversion of imprint images provides 'virtual casts' that assist in visualization and identification of the original nannofossils (Fig. 1). Imprints were found as single or multiple specimens of the same or different species and cover a range of forms, including small coccoliths (< 3 μm, Fig. S3I), larger nannoplankton (Figs. S3J-O and S8A-D) and collapsed coccolithophore exoskeletons (coccospheres) (Figs. S5A-B and S8F). Nannoplankton imprints on organic matter have only occasionally been reported from the fossil record (*13–15*), presumably because of their cryptic mode of preservation and minute size. Some studies have interpreted imprints as the negative molds of coccoliths that were dissolved during acid digestion of rock samples in the laboratory

(*14*). However, we record imprints on unprocessed rock surfaces (Fig. S6) and in samples devoid of $CaCO_3$, showing these fossils occur naturally.

Reduced nannoplankton abundances during the T-OAE have been reported from multiple locations (Data S1), but this signal is most extreme in the Cleveland Basin, Yorkshire (UK), where a nannoplankton 'disappearance event' has been observed (*16*). Samples from Yorkshire, studied here using traditional nannoplankton 'body' fossil methods, were either barren, or yielded 'rare' or 'very rare' nannofossils (Figs. S13 and S14). These observations essentially replicate previous findings of reduced species abundances or absences throughout the T-OAE (*17*), and seemingly support the biocalcification crisis paradigm. However, imprints from the same samples challenge this view, revealing abundant and rich nannoplankton communities throughout the T-OAE interval, refuting the 'disappearance event' hypothesis. Imprints are not just confined to the Cleveland Basin but have been discovered in a wide range of depositional settings in globally-distributed T-OAE strata (e.g. Germany, Japan and New Zealand, Figs. 1 and 2). These results indicate that observed decreases in $CaCO_3$ and nannofossil abundance through the T-OAE are due to $CaCO_3$ dissolution after burial, rather than representing a primary crisis of the living nannoplankton. The imprint fossils from Japan and New Zealand (Fig. 1) are the oldest coccoliths recorded from these countries, demonstrating that this approach is widely applicable and can expand nannofossil records, even in rocks where 'body' fossils are absent and have been subjected to thermal alteration (e.g. Japanese material studied here [*17*]).

We further extended our study to test for imprints through two Cretaceous OAEs, the early Aptian OAE1a (~120 Ma) and the Cenomanian-Turonian OAE2 (~94 Ma), for which there are also claims for biocalcification crises (reviewed in Data S2 and S3). The Cretaceous OAEs are also associated with distinct episodes of volcanism, and characterized by comparable suites of environmental, geological and ecological changes (*12* and references therein). We found imprint

fossils through both Cretaceous OAEs (Figs. 1 and 2, Figs. S11 and S12), demonstrating that 'ghost' nannofossil preservation is not limited to the T-OAE, and that observed decreases in $CaCO_3$ and nannoplankton abundances during OAE1a and OAE2 (Data S1 to S3) are likely also linked to the secondary removal of $CaCO_3$ from the rock record. Imprints from OAE2 of Contessa, Italy, are particularly important because these were recorded during an inferred nannoplankton biocalcification 'blackout', corresponding to the Bonarelli Level, a ~1-meter-thick black shale virtually devoid of $CaCO_3$, which abruptly interrupts a limestone succession rich in 'body' fossils (Fig. S14, Data S3). Our results overturn the blackout hypothesis and indicate that the original $CaCO_3$ has been lost through post-burial dissolution, leaving a misleading signal of declining carbonate production during OAE2.

The recurrence of imprints in OAE-related sediments demonstrates that these organic-rich intervals are especially prone to this type of nannofossil preservation, indeed the OAE intervals record the richest imprint assemblages. Abundances of imprints and AOM generally positively correlate (Fig. S15), suggesting that plentiful organic matter was an important requirement, providing the necessary 'plastic' substrate for imprinting. This also explains the subsequent dissolution of $CaCO_3$, as high organic matter content can lead to acidic pore waters during diagenesis (*18*). The formation of imprints also required overburden pressure prior to the loss of the 'body' fossils, indicating that dissolution took place after burial, and the absence of compressed imprints reveals that this occurred after lithification.

Nannofossil abundances in sedimentary rocks are the product of a range of factors, including those that affect original populations (temperature, nutrients, water chemistry), export pathways (grazing, ballasting), secondary abundances (exported plankton *versus* siliciclastic dilution) and preservation (diagenesis). None of these factors necessarily disrupts calcification in the living nannoplankton and therefore preserved abundance changes alone do not provide

evidence of biocalcification crises. On the contrary, our observations show that $CaCO_3$ and nannoplankton 'body' fossil abundances can be severely modified or eradicated following deposition, indicating that these records are unreliable proxies for OA or pelagic carbonate production. Independent geochemical proxy evidence for OA at the T-OAE remains contentious (*19*, *20*), and given the uncertainty over rates of carbon injection that drove this and other OAEs, these rates may well have been too slow to have induced prolonged or high magnitude surface water OA (*10*, *21*). However, regardless of the severity or duration of OA during the T-OAE, or indeed other proposed causes of a nannoplankton crisis, such as changes in temperature, salinity, nutrients or anoxia (see Data S1), our records challenge the concept of a crisis. More generally, these findings call for the re-examination of other inferred biocalcification crises, and 'ghost' nannofossils represent a tool with which to test such claims.

Our imprint record shows that nannoplankton communities were more resilient to the environmental changes during the T-OAE – including high-CO_2 and warming (evident from independent proxies; *12* and references therein) – than the traditional nannofossil and $CaCO_3$ records suggest. However, several previously observed species-specific changes, such as declines in *Schizosphaerella punctulata* and nannoconids during the T-OAE and OAE1a, respectively, may still represent primary responses of nannoplankton to environmental change (Data S1 and S2). At the community-level, however, the imprint record shows that nannoplankton flourished during the T-OAE, and their resilience is supported by observations of increased speciation rates and an absence of elevated extinctions at the T-OAE and OAE1a (Data S1 to S3).

The abundance of prasinophyte algae in many T-OAE intervals is seen as a rise to dominance at the expense of nannoplankton (*16*), but the close association of imprints and prasinophyte fossils observed here demonstrates that both groups coexisted or occurred in close

succession (e.g. Fig. 1C). Near-monospecific assemblages of prasinophytes during the T-OAE likely represent persistent algal blooms (*22*), and similarly, the monospecific concentrations of nannofossil imprints (Fig. 2F, Figs. S3B and S7A) are pellets or aggregates that provide snapshots of high-dominance communities. Rather than being considered casualties of the T-OAE, our findings indicate nannoplankton continued to draw down CO_2 and sequester carbon in seafloor sediments, which in the long-term likely expedited the termination of the event. However, high production, blooms and potential toxicity (*23*), suggest that in the short-term, like prasinophytes, nannoplankton fueled anoxia through eutrophication and increased accumulation of organic matter at the seafloor, enhanced by coccolith ballasting (*24*) (Fig. 3).

Our records of 'ghost' nannofossils, discovered using unconventional methods, indicate no evidence for biocalcification crises during the studied Mesozoic OAEs, at least for plankton that form calcite, the more stable $CaCO_3$ polymorph compared to aragonite. Instead, these findings show how diagenesis can completely reshape the geological archive and highlight that a literal reading of the fossil record can mislead interpretations. Given that atmospheric CO_2 concentrations are currently rising at unprecedented rates, the use of individual OAEs as past analogues of current change may be premature, because carbon-input rates – and therefore the duration and intensity of surface water OA – remain uncertain for these events (*10*, *21*). Nevertheless, our imprint record demonstrates the resilience of nannoplankton communities during multiple past global warming events, and equally, shows that plankton proliferation can accelerate the development of OAEs. Our findings also indicate that the conditions that prevailed during OAEs may become more prevalent (*25*, *26*), with plankton blooms and hypoxic dead zones becoming widespread across globally warming oceans.

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Supplementary Materials

Materials and Methods

Figs. S1 to S15

References (*27–74*)

Data S1 to S5

Figure Captions

Fig. 1. 'Ghost' nannofossils imprinted on organic matter. (**A**) *Staurolithites* sp. imprint on *Classopollis* spp. (pollen) [NHMUK PM FM 2355 (2)]. (**B**) *Crepidolithus impontus* imprints on *Cerebropollenites macroverrucosus* (pollen) [NHMUK PM FM 2355 (2)]. (**C**) *Bussonius prinsii* imprint on prasinophyte algae [NHMUK PM FM 2355 (2)]. (**D–K**) Imprints on amorphous organic matter. (**D**) *Bussonius prinsii* [NHMUK PM FM 2355 (2)]. (**E**) *Axopodorhabdus atavus* [NHMUK PM FM 2377 (1)]. (**F**) *Calyculus serrai* coccosphere [NHMUK PM FM 2377 (1)]. (**G**) *Axopodorhabdus* sp. [S043981]. (**H**) *Lotharingius hauffii* [S043957]. (**I**) *Calyculus* sp., *Staurolithites* sp. and others [S043993]. (**J**) *Manivitella pemmatoidea* [S043946]. (**K**) *Stoverius achylosus* [S043941]. Blue images are inverted 'virtual casts'. Scale bars in overviews of (A–C) are 10 μm, all other scale bars are 2 μm.

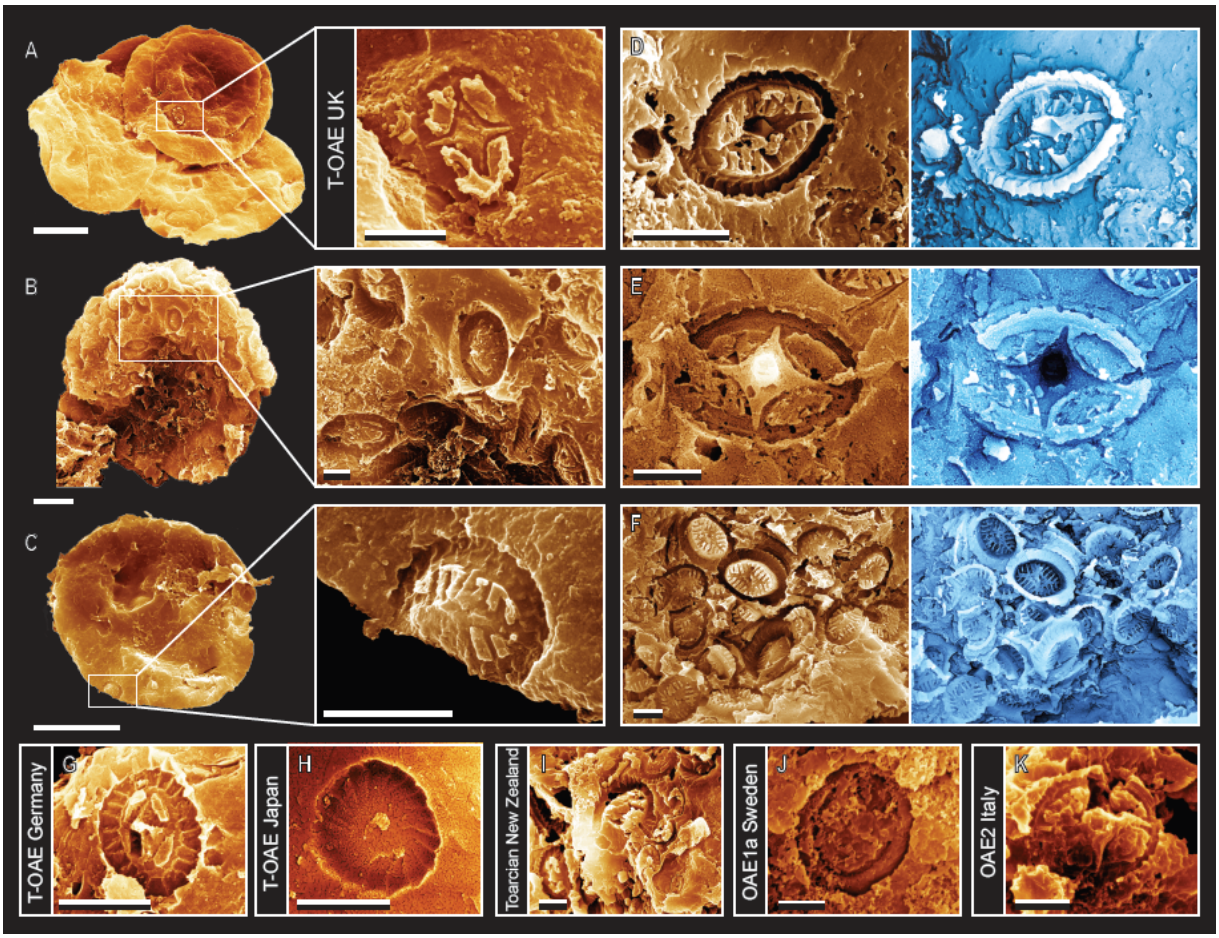

Fig. 2. 'Ghost' nannofossil, 'body' nannofossil and organic matter records through the T-OAE (Japan, UK), OAE1a (Sweden) and OAE2 (Italy). Imprints/area represents the number of imprints recorded across a standard area of organic matter. 'Body' fossil abundance categories: Abundant = >10% of particles; Common = >1–10%; Frequent = 0.1–1%; Rare = <0.1%; Very Rare = <20 specimens in total; Barren = no 'body' fossils. See Materials and Methods for further details, including richness and organic matter data collection methods. Note the different vertical scale for OAE2. See Fig. S14 for extended version that includes data from Germany and New Zealand. For raw data, see Data S4.

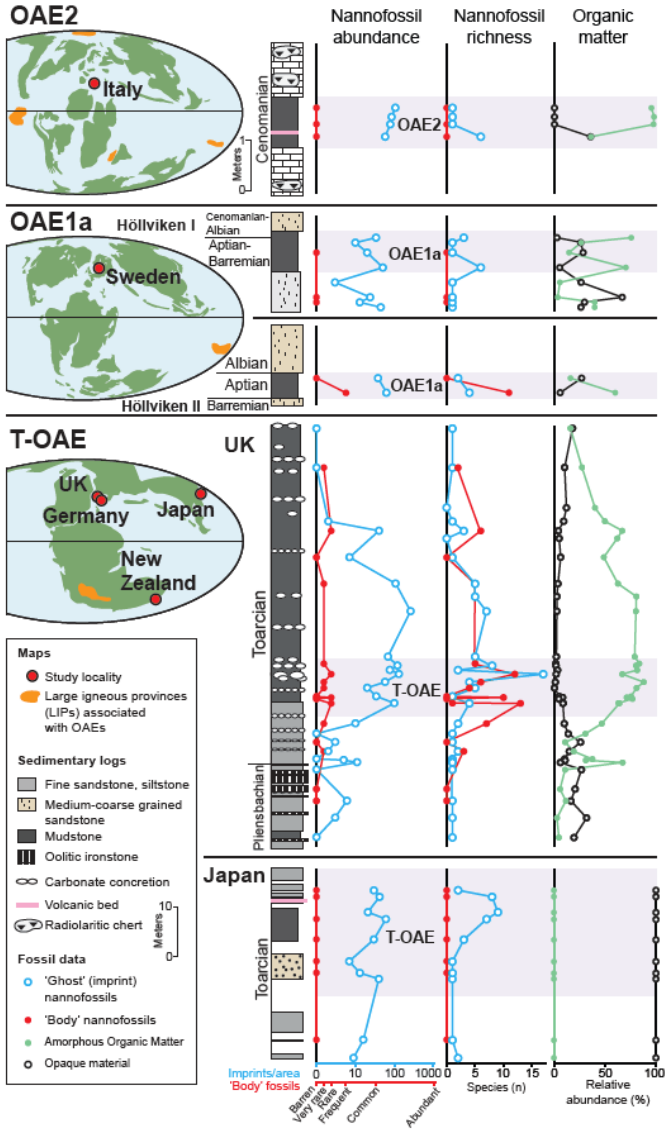

Fig. 3. Schematic summary of the major changes in phytoplankton groups through the T-OAE, showing changes in phytoplankton export and the formation of nannofossil imprints. OMZ = Oxygen minimum zone. Note the expansion of the oxygen minimum zone during the OAE, and the acidic pore waters within sub-surface sediments post-OAE leading to the dissolution of nannoplankton 'body' fossils and the formation of imprints.