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# Lower Jurassic conodonts from the Inuyama area of Japan: implications for conodont extinction

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It is generally accepted that conodonts went extinct at the end of the Triassic, but younger conodont fossils have been reported, and it is becoming clear that conodont extinction occurred asynchronously across different regions. Although some reports of post-Triassic conodonts have been disproven, Lower Jurassic conodonts have been found in the Buda area of Hungary and the Inuyama area of Japan. Here, we report the discovery of more conodonts *Misikella posthernsteini* above the first occurrence of the typical Jurassic radiolarian *Pantanellium tanuense*, which is not known from the Triassic, in the Kastuyama section, Inuyama area, reaffirming the authenticity of the Lower Jurassic conodonts. The conodonts survived into the Jurassic in the Inuyama area might be due to their remote locations relative to the Central Atlantic Magmatic Province, which buffered them from hypoxia and ocean acidification. Although conodonts survived into the Lower Jurassic, they failed to recover and quickly went extinct in post-extinction ecosystems. The “dead clades walking” (DCWs) of conodonts may have been due to protracted ocean acidification in the earliest Jurassic. Food scarcity and competition with other organisms may have led to the eventual extinction of conodonts.

## KEYWORDS

mass extinction, post-Triassic, T-J boundary, Lower Jurassic, conodonts

## Introduction

Conodonts are important index fossils in marine strata (Rigo et al., 2018; Tong et al., 2021). Although it is generally accepted that conodonts appeared in the Cambrian and went extinct at the end of the Triassic (Clark, 1983), some post-Triassic conodonts have been reported. For instance, Diebel (1956) reported “Upper Cretaceous” conodonts from West Africa; Nohda and Setoguchi (1967) reported “Upper Jurassic” conodonts from Japan. Although these two examples were later shown to be of Triassic age (Müller and Mosher, 1970), the reports had already attracted attention. Nonetheless, Kozur and Mock (1991) identified a new ramiform conodont *Neohindeodella detrei* in the Várhegy section (Buda, Hungary), and subsequent studies confirmed that its highest appearance in the Várhegy and nearby Csóvár sections is above Lower Jurassic radiolarians and ammonoids (Kozur, 1993; Pálffy et al., 2007; Götz et al., 2009; Korte and Kozur, 2011). Thus, *N. detrei* became the first confirmed ramiform conodont to have survived into the Early Jurassic. In addition, Hori (1997) found some conodonts in Toarcian (Lower

Jurassic) chert beds from southwestern Japan, but these post-Triassic conodonts are considered reworked. Recently, [Golding \(2020\)](#) reported a single conodont *Neohindeodella* sp. at the Grotto Creek section in southeast Alaska originated from the same bed as the first occurrence (FO) of the Hettangian ammonoid *Psiloceras* sp., but the age of *Neohindeodella* sp. has been assigned to Triassic-Jurassic boundary transition in [Caruthers et al. \(2022\)](#). [Du et al. \(2020\)](#) identified conodont species of the genus *Misikella* that appear above the FO of the Lower Jurassic radiolarian species, including *Pantanellium tanuense*, *Archaeocenosphaera laseekensis*, in the Katsuyama section, Inuyama, Japan.

The extinction of the conodonts is one of the most important events in the end-Triassic mass extinction (ETE). Studying the Lower Jurassic conodonts is thus important to both refining stratigraphy and understanding the extinction pattern of conodonts, and more broadly the ETE. Here, we review well-known reports of post-Triassic conodonts around the world and incorporate the newly discovered Lower Jurassic conodonts in the Katsuyama section to discuss the temporal pattern and mechanism of conodont extinction.

## Geological setting

The Katsuyama section (35°25'22"N, 136°58'16"E) is in the Inuyama area, central Honshu Island, Japan ([Figures 1B,C](#)). The entire

section is continuous, about 32 m thick, and comprises the Upper Triassic to the Lower Jurassic rhythmically layered siliceous rocks and shales ([Hori, 1990](#)). Single layers are typically 1–10 cm thick and exhibit different colors, including black, green, red, and purple ([Hori, 1992](#)). Upper Triassic strata are dominated by dark red siliceous rocks that transition into purple cherts and shales at the Triassic-Jurassic (T-J) boundary; the Lower Jurassic strata are red again ([Figure 2](#)). The layers of the T-J boundary in the Katsuyama section are about 3.5 m thick ([Figure 1D](#)).

During the Late Triassic to Early Jurassic, Inuyama was in a low-paleolatitude pelagic area of Panthalassa ([Figure 1A; Ando et al., 2001; Uno et al., 2015](#)), the deposition rate was very slow (1–7 mm/kyr), and the siliceous rocks were deposited below the carbonate compensation depth (i.e., at least 4,000 M depth; [Matsuda and Isozaki, 1991](#)).

[Hori \(1992\)](#) and [Carter and Hori \(2005\)](#) established globally comparable radiolarian biozones in the Katsuyama section: the *Globolaxtorum tozeri* Zone is the last Upper Triassic radiolarian zone and the T-J boundary is defined by their last appearance of this index species ([Carter and Hori, 2005](#)), although younger than the T-J boundary as defined by the FO of ammonoid *Psiloceras spelae tirolicum*. The first Lower Jurassic radiolarian zone is the *Pantanellium tanuense* Zone. [Ikeda and Tada \(2014\)](#) established an astronomical time scale (ATS) in the Inuyama area, and the Inuyama-ATS anchored at the end-Triassic radiolarian extinction event as  $201.4 \pm 0.2$  Ma, the

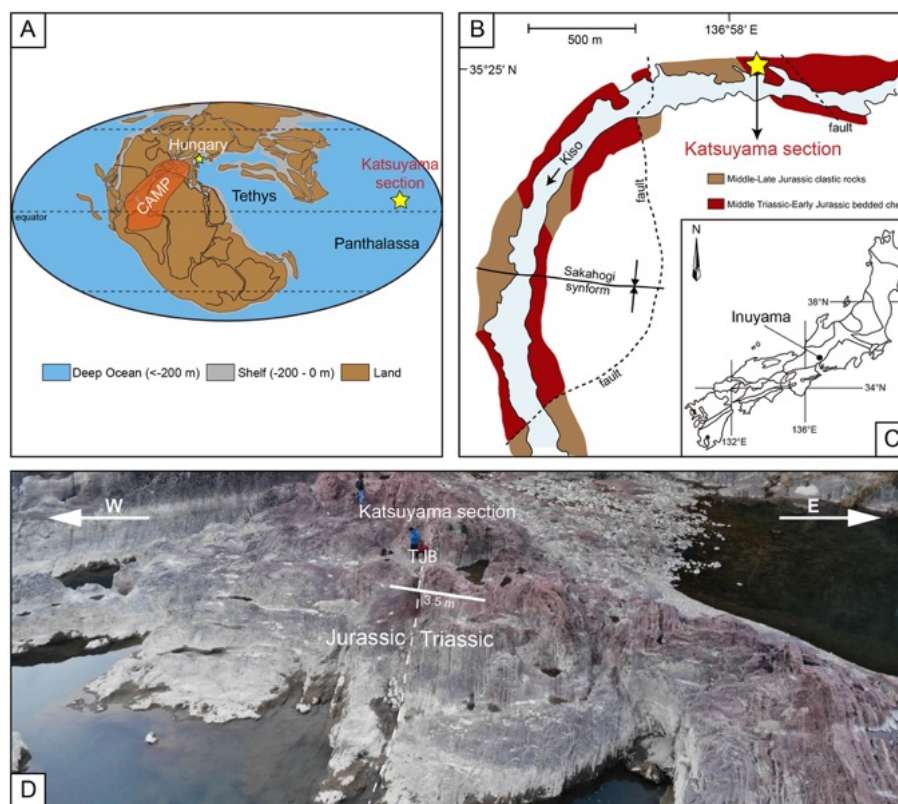
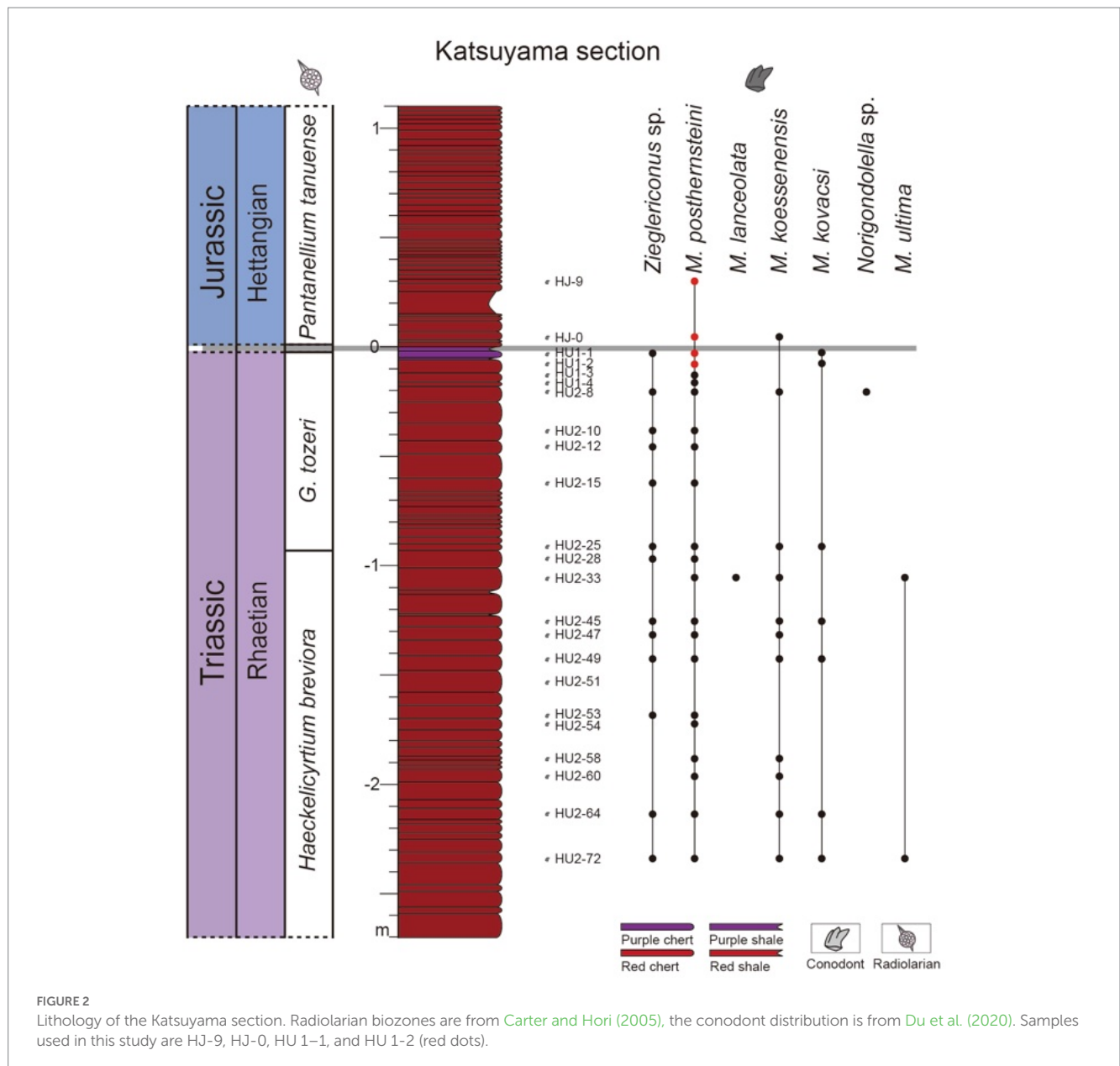


FIGURE 1

(A) Global paleogeographic map of the end Triassic (modified after [Du et al., 2020](#)); CAMP, Central Atlantic Magmatic Province. (B) Geological map of the Inuyama area (modified after [Fujisaki et al., 2018](#)). (C) Location of the Inuyama area in central Japan. (D) Annotated photograph of an outcrop of the Katsuyama section; TJB, Triassic-Jurassic boundary.



age was revised in Bôle et al. (2022) as  $201.57 \pm 0.2$  Ma. Du et al. (2020) identified pectiniform conodonts *Zieglericonus* sp., *Norigondolella* sp., *Misikella posthernsteini*, *M. lanceolata*, *M. koessenensis*, *M. kovacsi*, and *M. ultima* in the Katsuyama section, as well as some ramiform conodont elements. Some *M. posthernsteini* and *M. koessenensis* are found above the FO of the Lower Jurassic radiolarian *P. tanuense* (Figure 2).

Organic carbon isotope profiles have been established in the Inuyama area (Kuroda et al., 2010; Okada et al., 2015; Fujisaki et al., 2018). Okada et al. (2015) and Fujisaki et al. (2018) obtained the organic carbon isotope data from cherts and mudstones respectively, but the results of them are obviously different. The values in Fujisaki et al. (2018) are more scattered, from  $-29.07\text{‰}$  to  $-21.10\text{‰}$ . They identified three prominent negative carbon isotopic excursions (NCIEs) in the Katsuyama section and correlated these three NCIEs, respectively, with the precursor, initial, and main CIEs in the Tethys.

However, the  $\delta^{13}\text{C}_{\text{org}}$  values obtained by Okada et al. (2015) from cherts are relatively stable, ranges from  $-25.7\text{‰}$  to  $-24.1\text{‰}$ . The reasons for this difference still need further studies and discussions.

## Materials and methods

The new conodonts reported herein were found in chert samples HJ-9, HJ-0, HU 1-1, and HU 1-2 collected from the Katsuyama section in 2019 (Figure 2). About 100 grams of cherts per sample were dissolved in hydrofluoric acid at Kyushu University, Japan, following the method described by Yamashita et al. (2018). Conodonts were picked from the sorted residue under binocular stereoscope. The conodonts are now preserved in the Laboratory of Paleooceanography, Paleoclimate and Paleontology, Institute of Sedimentary Geology, Chengdu University of Technology.

## Results

Seventeen conodonts were collected from the Jurassic samples. Most of the conodonts are not particularly well preserved, but some can be identified at species level and consist in *Misikella posthernsteini* and *M. posthernsteini?* from samples HJ-9, HJ-0, HU 1-1, and HU 1-2 (Figure 3).

Conodonts in samples HJ-9 and HJ-0 were stratigraphically above the FO of the Lower Jurassic radiolarian *Pantanellium tanuense* (Figure 2). The positions of sample HJ-0 and HJ-9 are about 6 cm and 33 cm higher than the FO of *P. tanuense*, respectively. Du et al. (2020) had already described Lower Jurassic conodonts *M. posthernsteini* and *M. koessenensis* at the levels of HJ-9 and HJ-0. Here, we report the discovery of more conodonts above the *P. tanuense* from the Kastuyama section, it is a supplement to the study of Jurassic conodonts in the Inuyama area,

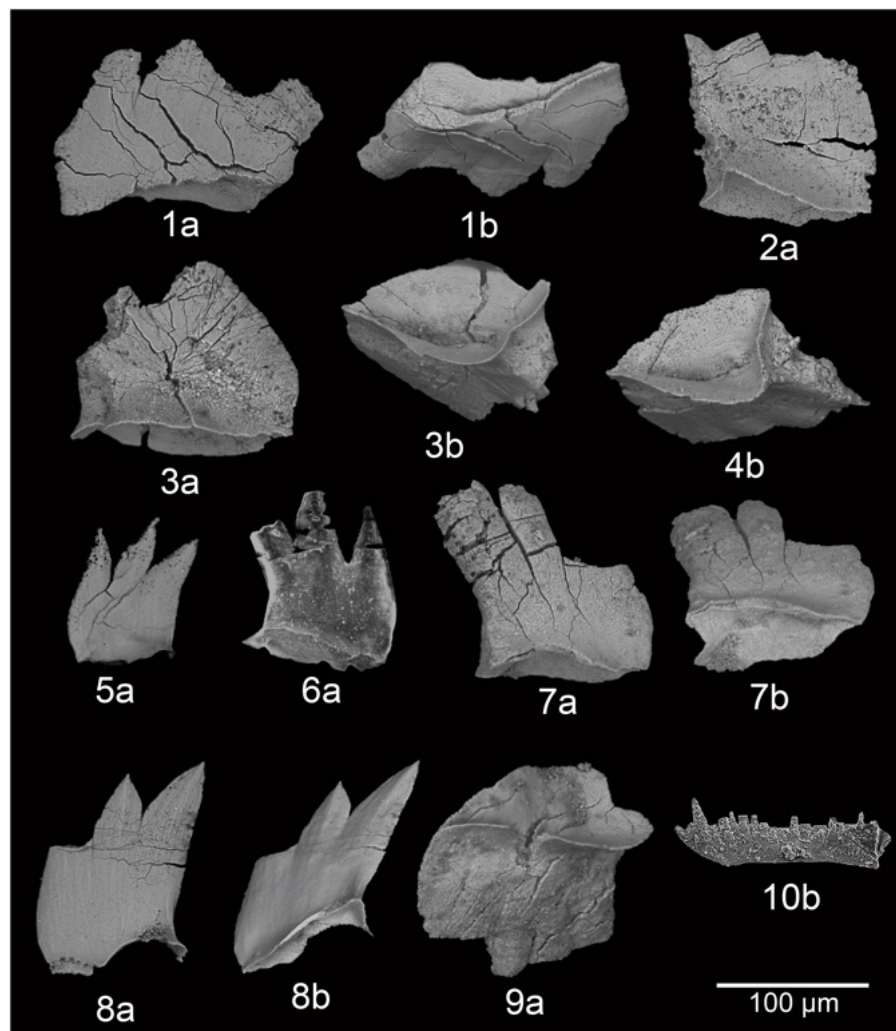
also reaffirming the authenticity of the Lower Jurassic conodonts in the study area.

## Discussion

### Reported post-Triassic conodonts

#### “Post-Triassic” conodonts from West Africa and Japan

Diebel (1956) reported conodonts from West Africa to be of Late Cretaceous in age based on an individual ammonoid fossil found with them. However, the most abundant species they discovered were “*Polygnathus mungoensis*” and *Enantiognathus zieglerei*. Mosher (1968) reclassified “*P. mungoensis*” into the genus *Epigondolella*, which is abundant in Ladinian (Middle Triassic)



**FIGURE 3**  
SEM photos of conodonts from the Kastuyama and Csóvár sections; a and b indicate lateral and lower views, respectively. (1, 3) *Misikella posthernsteini?*, HJ-0; (2, 4) *Misikella posthernsteini*, HJ-0; (5) *Misikella posthernsteini*, HU 1-2; (6) *Misikella posthernsteini*, HU 1-1; (7) *Misikella posthernsteini*, HJ-9; (8, 9) *Misikella posthernsteini* from Du et al. (2020); (10) *Neohindeodella detrei* from Pálffy et al. (2007).

rocks in some areas of the United States and Canada. Currently, *mungoensis* has again been reclassified into the genus *Budurovignathus*, and it is a typical representative of the Ladinian to lower Carnian. *Enantiognathus zieglerei* was thought to be a ramiform conodont that appeared throughout the Triassic. However, Koike (2004) suggested that *E. zieglerei* may be the S1 element of *B. mungoensis*. Therefore, conodonts from West Africa generally do not belong to the Upper Cretaceous, but the Middle Triassic to lower part of Upper Triassic.

Nohda and Setoguchi (1967) reported the Upper Jurassic conodonts in Japan, but they were proven to be the Triassic conodont *Epigondolella abneptis*. *Epigondolella abneptis* was originally discovered in Anisian (Middle Triassic) to Norian (Upper Triassic) strata (Huckriede, 1958), but the original description was insufficiently detailed and many conodonts with distinct morphological characteristics were misclassified as *E. abneptis* (Karádi, 2018). Therefore, Moix et al. (2007) described *E. abneptis* in more detail, and now it has a confirmed age range limited to the Norian, in the Upper Triassic (Karádi, 2018). Nohda and Setoguchi (1967) found these Triassic conodonts from a limestone block in the Jurassic accretionary complex (Chichibu Belt) because they did not realize that the limestone is included as an extraneous block in the melange complex.

Furthermore, conodonts, especially pectiniform elements, evolved rapidly, so it is highly unlikely that morphological characteristics could have remained unchanged from the Triassic to the Upper Jurassic, much less the Upper Cretaceous (Müller and Mosher, 1970). In addition, determinations that conodonts are post-Triassic age must be confirmed by other coeval fossils and/or reliable chronological markers.

### Lower Jurassic conodonts from Hungary

Kozur and Mock (1991) established two important Upper Triassic conodont species in the Várhegy section. The first, *Misikella ultima* ('the last *Misikella*'), is an important conodont element of middle-late Rhaetian age that roughly corresponds to the Upper Triassic ammonoid *Choristoceras marshi* Zone. The second is the ramiform *Neohindeodella detrei*, the highest occurrence of which is above the uppermost Triassic ammonoid *Choristoceras*. Accordingly, Kozur and Mock (1991) defined the age of *N. detrei* as late Rhaetian to early Hettangian (Early Jurassic), and Kozur (1993) subsequently identified other *N. detrei* above Lower Jurassic radiolarians, indicating that some *N. detrei* survived into the Hettangian (Figure 4C). Continued research in the Várhegy and Csövár sections found that the highest occurrence of *N. detrei* is above the Lower Jurassic ammonoid *Psiloceratids* indet. and radiolarian *Canoptum merum* (Kozur, 1993; Pálfy et al., 2007; Götz et al., 2009; Korte and Kozur, 2011). *Neohindeodella detrei* is the first conodont to have been extant into the Lower Jurassic before the discovery of the Lower Jurassic conodonts in the Katsuyama section (Japan).

However, the certainty of the Jurassic age of the conodonts *N. detrei* has always been controversial. First, the age of radiolarian *C. merum* is not considered exclusively Jurassic, Tekin et al. (2020) presents a range of Rhaetian to lower Sinemurian for this radiolarian in southern Turkey. Second, poor preservation hinders firm identification of ammonoids (Pálfy et al., 2007). Third, the presence of slump structures in the section cast doubt on whether *N. detrei* truly extended into the Lower Jurassic (Pálfy et al., 2007).

### Lower Jurassic conodonts from Alaska

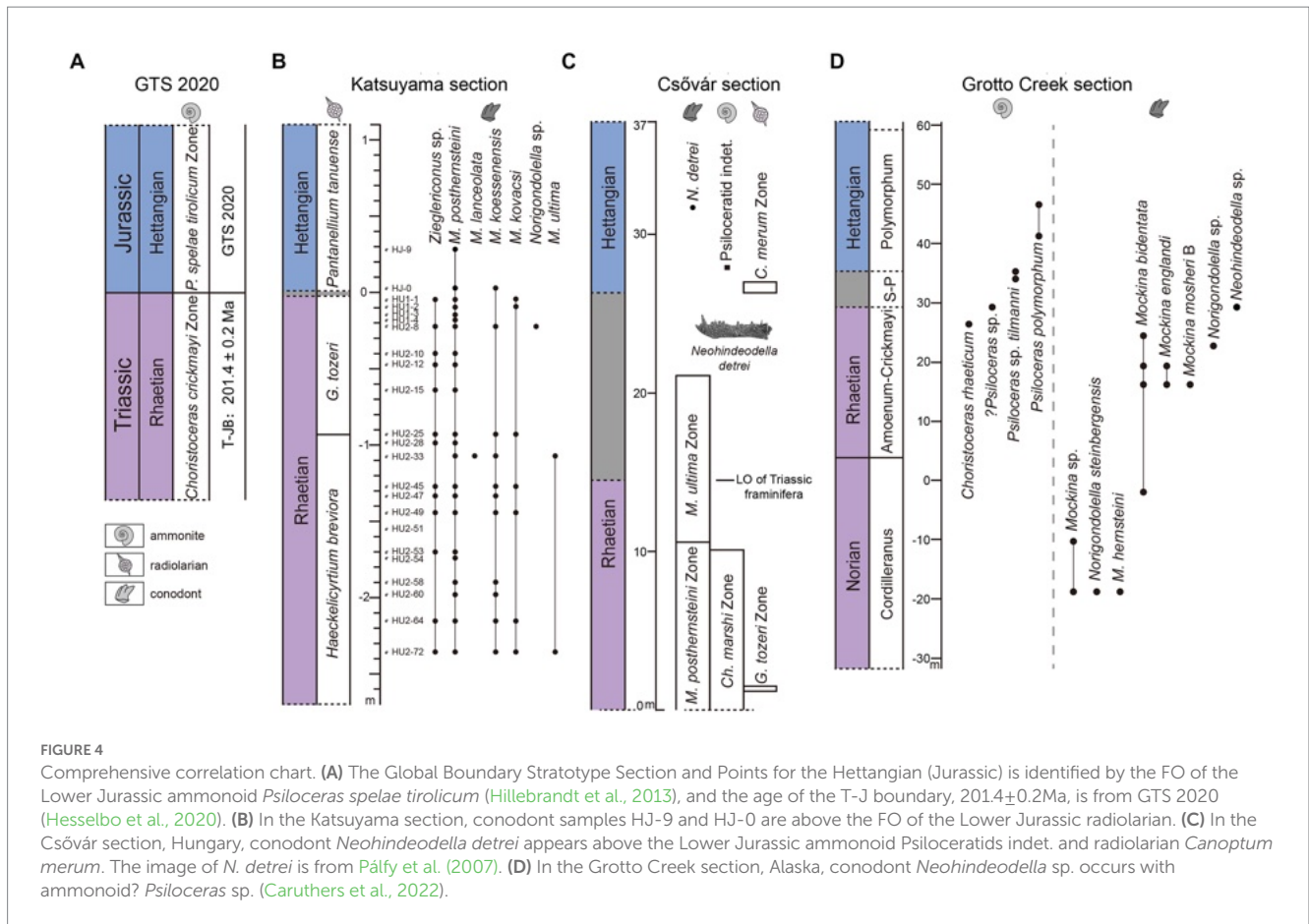
Golding (2020) reported conodonts from the Norian to Hettangian in the Grotto Creek section in southeast Alaska. The highest conodont sample corresponds to the same bed where the Hettangian ammonoid *Psiloceras* sp. first occurs, and included a single conodont specimen referred to *Neohindeodella* sp. The discovery of an additional specimen of the same genus *Neohindeodella* as in Hungary from Jurassic rocks at a different location likely suggested that conodonts did survive into at least the earliest Hettangian. However, Caruthers et al. (2022) thinks the classification of ammonoid *Psiloceras* sp. is dubious, they reclassified it as ?*Psiloceras* sp. Therefore, the Jurassic age of the ammonoid ?*Psiloceras* sp. and conodont *Neohindeodella* sp. originated from the same bed as the ammonoid ?*Psiloceras* sp. is uncertain. In the Grotto Creek section, there is a stratigraphically continuous T-J boundary transition interval from meter 29.42 to 35.46 between the bed with the ammonoid ?*Psiloceras* sp. along with conodont *Neohindeodella* sp., and the ammonoid *Psiloceras* cf. *tilmanni* (Figure 4D). The reclassification of ?*Psiloceras* sp. makes the Jurassic age of *Neohindeodella* sp. uncertain, but does not rule out the possibility that *Neohindeodella* sp. belongs to the Lower Jurassic.

### Lower Jurassic conodonts in the Inuyama area of Japan

In the Katsuyama section, the T-J boundary is generally defined by radiolarians due to the lack of ammonoid fossils. However, the radiolarian-defined T-J boundary is inconsistent with the standard T-J boundary based on ammonoids. Therefore, although it can be confirmed that some pectiniform conodont elements in the Katsuyama section are Lower Jurassic based on their occurrence relative to Hettangian radiolarians, it is necessary to discuss the radiolarian-defined T-J boundary in the Katsuyama section.

When the International Subcommittee on Jurassic Stratigraphy decided the primary marker of the T-J boundary, they included the ammonoid *Psiloceras spelae* (Ferguson Hill section, United States, and Kuhjoch East section, Northern Calcareous Alps, Austria), the ammonoid *Psiloceras planorbis* (St. Audrie's Bay section, England, and Waterloo Bay section, Northern Ireland), a major evolutionary replacement of radiolarian fauna (Kunga Island section, Queen Charlotte Islands, Canada), and a carbon isotopic excursion (Ferguson Hill section). *Psiloceras spelae* from the Kuhjoch East section was eventually selected as the primary marker (Hillebrandt et al., 2013). Therefore, the Global Boundary Stratotype Section and Point (GSSP) for the Hettangian is now the FO of primary marker ammonoid *Psiloceras spelae tirolicum* in the Kuhjoch East section (Figure 4A; Hillebrandt et al., 2013). However, a numerical age has not been obtained in the Kuhjoch East section to constrain the age of the T-J boundary.

Numerous radiometric ages have been reported from North American tuff layers produced by the Central Atlantic Magmatic Province (CAMP), along with biostratigraphic age constraints. For example, Schoene et al. (2010) measured a zircon age of  $201.33 \pm 0.13$  Ma in a tuff layer 1.5 m above the FO of *P. spelae* in the New York Canyon section and they also estimated the age of the T-J boundary in the Pucara section, Peru, to be  $201.31 \pm 0.18$  Ma based on radiometric ages above and below the FO of ammonoid *P. spelae*. Guex et al. (2012) also obtained a zircon U-Pb age of  $201.45 \pm 0.14$  Ma in a tuff layer 4.5 m below the FO of *P. spelae* in the Pucara section.



Hillebrandt et al. (2013) estimated the mean age of the T-J boundary to be 201.3 Ma based on previous studies. Subsequently, Hesselbo et al. (2020) combined multiple datasets to estimate the age of the T-J boundary to be  $201.4 \pm 0.2$  Ma in the Geologic Timescale (GTS) 2020 (Figure 4A).

Although not selected as the primary marker of the T-J boundary, the evolutionary turnover of radiolarian fauna remains a landmark event across the T-J boundary transition. Indeed, changes in radiolarian fauna have been used to define the T-J boundary in regions where ammonoids are absent. The Kunga Island section was a candidate section for the Hettangian GSSP based on the major evolutionary replacement of radiolarian fauna at the T-J boundary (Hillebrandt et al., 2013). There, the change of radiolarian fauna is represented by the disappearance of the Upper Triassic radiolarian *Globolaxtorum tozeri*. However, the ammonoid-defined T-J boundary is higher than the highest occurrence of *G. tozeri*. There is thus a brief interval between the disappearance of *G. tozeri* and the FO of the Lower Jurassic radiolarians *Canoptum merum* and *Pantanellium tanuense* in the Kunga Island section, and the exact position of the T-J boundary could not be determined there due to the absence of ammonoid *P. spelae*.

In the Katsuyama section, the T-J boundary was also defined based on radiolarians due to the absence of ammonoids since the basin was deposited below the CCD. Previous studies have established high-precision radiolarian zones in the Inuyama area (Hori, 1988, 1992; Carter and Hori, 2005; Hori et al., 2007), including *G. tozeri* Zone for the upper Rhaetian and *P. tanuense* Zone for the lower

Hettangian (Carter and Hori, 2005). Carter and Hori (2005) correlated radiolarian assemblages in strata near the T-J boundary between Queen Charlotte Islands and Inuyama. Although the environments and depositional rates of the two regions differ, the evolutionary patterns of radiolarian species are quite similar, and radiolarian zones are well correlated: the Rhaetian *G. tozeri* Zone in the two regions correspond directly, and the Hettangian *C. merum* Zone in Queen Charlotte Islands corresponds to the Hettangian *P. tanuense* Zone in the Inuyama area (Carter and Hori, 2005). Ikeda and Tada (2014) established an astronomical time scale (ATS) in the Inuyama area, and the Inuyama-ATS anchored at the end-Triassic radiolarian extinction event as  $201.4 \pm 0.2$  Ma, and recently this age has been revised as  $201.57 \pm 0.2$  Ma (Bôle et al., 2022). In the Katsuyama section, there was also a brief period of transition between the disappearance of *G. tozeri* and the first appearance of the Lower Jurassic radiolarian *P. tanuense*. The ammonoid-defined T-J boundary might be later than the last appearance of *G. tozeri* and predate the FO of *P. tanuense* in the Katsuyama section.

In general, the radiolarian zones on either side of the T-J boundary in the Katsuyama section are well correlated to coeval radiolarian zones of the Kunga Island section (Carter and Hori, 2005). More importantly, the conodonts found in the Katsuyama section not only occurred above the radiolarian-defined T-J boundary, but also above the base of the *P. tanuense* Zone. The conodonts occurred beyond the first appearance of Hettangian radiolarians, such as *P. tanuense*, *Archaeocenosphaera laseekensis*, *Amuria impensa*, *Praehexasaturnalis tetradradiatus*,

*Spongotrochus?* sp. sensu Carter (1994) and some primitive species of *Charlottea*, *Parashuum*, *Udalia* in the Katsuyama section.

Du et al. (2020) collected two elements of the genus *Misikella* (i.e., *M. posthernsteini* and *M. koessenensis*) in Lower Jurassic strata of the Katsuyama section, at positions HJ-9 and HJ-0, respectively. Herein, we collected more *M. posthernsteini* from samples HJ-9 and HJ-0, and the highest appearance of *M. posthernsteini* was about 0.33 m above the FO of the Hettangian radiolarian *P. tanuense* (Figure 4B). In the western Tethys, Rigo et al. (2018) identified the FO of *M. posthernsteini* as a marker for the base of the Rhaetian stage. In North America, *M. posthernsteini* apparently occurs in the middle–late Rhaetian (Orchard et al., 2007). *Misikella posthernsteini* is generally believed to have survived until the end of the Triassic, for instance in the Inuyama area of Japan, British Columbia of Canada and Steinbergkogel of Austria (Krystyn et al., 2007; Orchard et al., 2007; Ikeda and Tada, 2014). Actually, the duration of this conodont is longer than previously known. The records in the Katsuyama section indicate that some *M. posthernsteini* survived also into the Lower Jurassic.

It is important to mention that Hori (1997) first reported conodonts that occasionally occurred in Toarcian (Jurassic) bedded chert from the Inuyama areas in Japan. The reported conodonts are very similar to the Triassic forms according to Hori (1997). However, the Toarcian radiolarian biostratigraphy reveals that the conodonts could be reworked, because it is unlikely that Triassic conodonts suddenly appeared in Toarcian strata. Nevertheless, the strata of the studied T-J boundary section are continuous and without a clear depositional discontinuity, and any intraclast grains have been not found in the samples yet. Significantly, the conodonts found in the Katsuyama section occurred continuously from the Upper Triassic to the Lower Jurassic strata and the radiolarian biostratigraphy of the T-J boundary Katsuyama section is well-correlated with other regions, highlighting that there is no evidence that the Lower Jurassic (Hettangian) conodonts might have been reworked.

## Implications for conodont extinction

During the ETE, one of the five Phanerozoic mass extinction events (Hallam, 1996), a large number of marine and terrestrial organisms were affected or went extinct (McElwain et al., 1999, 2009). The extinction of the conodonts might be the most remarkable event of the ETE, and there are three outstanding questions regarding their extinction. What was the main reason for their extinction, and when and how (i.e., by what mechanism) did it occur?

As one of the most remarkable events of the ETE, the cause of conodont extinction remains debated. The most widely accepted hypothesis is that multiple pulses of the CAMP caused the larger ETE (Marzoli et al., 1999; Schlische et al., 2003) and directly led to the extinction of the conodonts (Fujisaki et al., 2018).

Most of the mass extinctions and some of the biotic turnover events are associated with perturbations of the carbon cycle (Fox et al., 2020). It has also been recorded during the T-J boundary transition. The prevailing view is that the massive exogenous isotopically light carbon from the emplacement of CAMP resulted the profound perturbations in the carbon cycle (Hesselbo et al., 2002; Pálffy et al., 2007; Thibodeau et al., 2016; Fujisaki et al., 2018; Du et al., 2020). Three NCIEs occurred in both the Tethys and Panthalassa and they are considered to have resulted from global carbon perturbations due

to CAMP volcanism (e.g., Hesselbo et al., 2002; Thibodeau et al., 2016; Fujisaki et al., 2018; Du et al., 2020). Fujisaki et al. (2018) identified three NCIEs, NCIE1, NCIE2, and NCIE3, in the Katsuyama section, and proposed that the three NCIEs correspond to the precursor, initial, and main CIEs in the Tethys, respectively. Based on global well-correlation of these three NCIEs, Du et al. (2020) considered that the three NCIEs were synchronous in the Tethys, eastern-Panthalassa and mid-Panthalassa. By using these three NCIEs as a calibration to establish the temporal pattern of conodont extinction event, conodonts disappeared at the end of the Upper Triassic in most areas (i.e., below the T-J boundary), but survived into the Lower Jurassic in the Buda and Inuyama areas (Du et al., 2020). However, although the three well-known global NCIEs are accepted by most people, another view considers that the NCIEs, especially for the initial-NCIE is not necessarily global (Fox et al., 2020; Bôle et al., 2022). Fox et al. (2020) used biomarker and compound specific carbon isotopic data in the Bristol Channel Basin (United Kingdom) where the iconic initial-NCIE was first observed demonstrated that the initial-NCIE is a record of microbial-mat development and other ecological changes driven by regional sea-level change, not because of the input of massive exogenous isotopically light carbon. Similarly, Okada et al. (2015) studied the carbon isotope from cherts in the Inuyama area show a different result compared with Fujisaki et al. (2018). Although there is debate of organic carbon isotope studying, it does not affect the conclusion that the extinction of conodont was asynchronous since the calibration is not only based on the organic carbon isotope curves, but also supported by integrated biostratigraphy of ammonoids, radiolarians, and palynomorphs (Du et al., 2020).

The mechanism by which CAMP volcanism caused conodont extinction remains debated. One view is that the large amounts of greenhouse gases (e.g., CO<sub>2</sub>) released by the CAMP resulted in global warming that ultimately led to the extinction of conodonts and other organisms (McElwain et al., 2005; Korte et al., 2009; Schaller et al., 2012; Blackburn et al., 2013). In this context, conodonts in shallow environments or near the eruptions should have been the first affected, whereas those in deep waters, benthic habitats, or environments far from the CAMP would only have been affected after some delay. However, the degree to which the release of greenhouse gases by CAMP volcanism affected global temperatures remains to be demonstrated (Du et al., 2020). The second possibility is that a widespread perturbation of the oceanic nitrogen cycle resulted in reduced nitrogen availability, limiting productivity throughout the oceans. However, existing evidence indicates that nitrogen cycle disturbances at the end of the Triassic were only regional (Schoepfer et al., 2016). Therefore, unless a global nitrogen cycle perturbation can be demonstrated, it is unlikely that regional nitrogen cycle perturbations could have led to the global extinction of conodonts. The third possible mechanism is ocean hypoxia. Biomarker tests indicate that some regions of the western Tethys and Panthalassa became hypoxic during the Late Triassic (Ricoch et al., 2012; Jaraula et al., 2013; Kasprak et al., 2015; Schoepfer et al., 2016; Fox et al., 2022). However, major, trace, and rare earth element analyses have confirmed that the middle of Panthalassa remained oxic during the late Rhaetian to the T-J boundary transition (Fujisaki et al., 2018). Therefore, the living conditions there should have been suitable for conodont survival. Furthermore, most Upper Triassic conodonts, including *Misikella*, have been proved to be surface

dwellers (Rigo and Joachimski, 2010; Rigo et al., 2012; Trotter et al., 2015) and it is unlikely that reducing conditions might have set on the upper zone of the column water. Another hypothesis is that ocean acidification caused conodont extinction. The large amount of CO<sub>2</sub> released by CAMP volcanism may have led to seawater acidification in some areas of the western Tethys and Panthalassa (Hautmann, 2004; Ikeda et al., 2015), and the ensuing unfavorable conditions, e.g., food scarcity, may have propagated the impacts to conodonts worldwide. Fujisaki et al. (2018) proposed that the ocean acidification and recurring shallow-marine anoxia events which caused by protracted CAMP volcanisms may place environmental stresses on the biosphere and eventually resulted in the end-Triassic biotic crisis. Fox et al. (2022) used high-resolution biomarker and compound-specific isotope revealed that the intensive euxinia and acidification driven by CAMP formed a two-pronged kill mechanism at the ETE. This also could be the mechanism of conodont extinction.

However, why some conodonts survived into the Lower Jurassic in the Buda and Inuyama areas remains unclear. In the Buda area, *N. detrei* was collected above the FO of a typical Jurassic psiloceratid ammonoid in the Csóvár section (Pálffy et al., 2001). Unfortunately, those *N. detrei* specimens are uniquely S elements of an unknown conodont apparatus and are never found associated with P and M elements, so very little information is available about the conodont's lifestyle. Despite the lack of sufficient knowledge about *N. detrei*, one possible reason for their survival into the Jurassic in the Buda area is that they lived in a restricted basin environment near the Dachstein carbonate platform (Haas et al., 1995; Pálffy et al., 2007) and were thus less affected by global events. Nonetheless, some outstanding questions about *N. detrei* remain. For example, why have they only been identified in the Buda area, and why have no P and/or M elements been found?

The Inuyama area was in the middle of Panthalassa during the Late Triassic. Although shallow marine areas were anoxic during the T-J boundary transition, the seawater remained oxic in pelagic areas such as Inuyama (Ikeda et al., 2015; Fujisaki et al., 2018). Nonetheless, the effects of ocean acidification were inevitable. The combination of ocean acidification and marine anoxia events can explain the biotic crisis at the end of Triassic, but cannot explain why conodonts in the Inuyama area survived longer than other places in the same environment. In addition, *Misikella* were surface-water dwellers (Trotter et al., 2015) and would have been affected by both ocean acidification and hypoxia. The explanation may be that, because the Inuyama area was in an open sea environment far from the CAMP, hypoxia and ocean acidification were less severe than areas closer to the CAMP. This relatively less harsh environment may have sustained these conodonts into the Lower Jurassic.

## The “dead clades walking” of conodont

Based on the Lower Jurassic conodonts discovered so far, both *Neohindeodella* and *Misikella* were extant from the Upper Triassic to the Lower Jurassic. Yet, no exclusively Jurassic conodonts have been found. Thus, another outstanding question is why those conodonts went extinct instead of slowly recovering like conodonts that survived the end-Permian mass extinction. The phenomenon of clades survives

major extinction event, but fail to recover and very quickly goes extinct in post-extinction ecosystems is called “dead clades walking” (DCWs), this term coined by Jablonski (2002). The DCWs of conodont is an issue worthy of further study. Conodonts suffered several extinctions and faunal turnovers from the Carnian (Upper Triassic) to the end of Triassic before their final extinction (Rigo et al., 2018; Du et al., 2021). One of the main events was in the late Julian (early Carnian), during which only few conodonts survived beyond that event (Kozur, 1989; Rigo et al., 2007). Afterwards, the diversity of conodonts began to recover, more than ten genera of pectiniform conodont (e.g., *Mazzaella*, *Carnepigondolella*, *Metapolygnathus*, *Mockina*, *Ancyrogondolella*, *Epigondolella*, *Orchardella*, *Zieglericonus*, *Parvigondolella*, *Norigondolella*, *Misikella*) appeared. However, only three genera (*Zieglericonus*, *Norigondolella*, *Misikella*) of them appeared at the end of the Triassic, and finally only *Misikella* survived the ETE to the lowermost Jurassic, but it also became extinct soon. Compared with *Zieglericonus* and *Norigondolella* in the same environment, the advantage of *Misikella* was that the diversity of species was more abundant (Figure 2), whether it was in the Inuyama area or other regions. Therefore, it had a greater advantage in the competition for survival, allowing it to survive until the Lower Jurassic. The eventual extinction of conodont survivors in the Early Jurassic may have been due to protracted ocean acidification from the end Triassic to the earliest Jurassic (Fujisaki et al., 2018). Bôle et al. (2022) observed two negative silicon isotope excursions (NSIEs) within the end-Triassic radiolarian turnover interval, and it could reflect the drops of radiolarian productivity. In fact, the main anomaly in these NSIEs occurred within ~1 mm interval, implying <kyr or up to decadal scale drastic environmental perturbation across the T-J extinction interval. This may also be one of the factors resulting in the extinction of conodonts.

In general, there were various adverse environmental factors in the Inuyama area during T-J boundary transition that may have led to the eventual extinction of conodonts or the disappearance of other organisms. However, its specific mechanism remains to be clarified.

## Conclusion

We reported the Upper Triassic and Lower Jurassic conodonts *Misikella posthernsteini* in four siliceous rock samples from the Katsuyama section (Inuyama area, Japan). The conodonts in samples HJ-9 and HJ-0 occur above the radiolarian-defined T-J boundary and the FO of the typical Lower Jurassic radiolarian *Pantanellium tanuense*, especially conodonts in the sample HJ-9 are about 33 cm above the *P. tanuense*. Therefore, these conodonts must have been extant in the Lower Jurassic. Although we did not find Lower Jurassic *M. koessenensis* like Du et al. (2020), these Lower Jurassic *M. posthernsteini* reaffirm the existence of Hettangian conodonts in the Inuyama area. The reason why some conodonts survived into the Lower Jurassic might be that the remote locations of the Inuyama area relative to the CAMP buffered them against hypoxia and ocean acidification resulting from protracted volcanism, allowing them to survive beyond the T-J boundary. The DCWs of conodont may have been due to protracted ocean acidification, food scarcity and competition with other organisms may have led to the eventual extinction of conodonts.



## Author contributions

YD conceived and designed the project. TO, YT, QW, and MR wrote the manuscript. All authors contributed to the article and approved the submitted version.

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## Conflict of interest

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