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Research paper

Re-discovery of a "living fossil" coccolithophore from the coastal waters of Japan and Croatia

Kyoko Hagino [a,b,*], Jeremy R. Young [c], Paul R. Bown [c], Jelena Godrijan [d], Denise K. Kulhanek [e], Kazuhiro Kogame [f], Takeo Horiguchi [f]

[a] Institute for Study of the Earth's Interior, Okayama University, Yamada, Misasa, Tottori 682-0193, Japan
[b] Research and Education Faculty, Natural Sciences Cluster, Sciences Unit, Kochi University, Akebono-cho 2-5-1, Kochi 780-8520, Japan
[c] Dept. of Earth Sciences, University College London, Gower St., London WC1E 6BT, United Kingdom
[d] Centre for Marine Research, Ruđer Bošković Institute, 52210 Rovinj, Croatia
[e] International Ocean Discovery Program, Texas A&M University, College Station, TX 77845, USA
[f] Department of Natural History Sciences, Faculty of Science, Hokkaido University, N10W8, Sapporo 060-0810, Japan

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ABSTRACT

The extant coccolithophore *Tergestiella adriatica* Kamptner, which had not been reported since its original description in 1940, was recently re-discovered in coastal-nearshore waters at Tomari, Tottori (Japan) and offshore Rovinj (Croatia). Morphological analysis shows that extant *Tergestiella* and the Mesozoic genus *Cyclagelosphaera* (Watznaueriaceae), thought to have been extinct since the early Eocene (~54 Ma), are virtually identical. Molecular phylogenetic study supports the inference that *T. adriatica* is a direct descendent of *Cyclagelosphaera*. It is therefore a remarkable example of a living fossil. Our documentation of patchy coastal distribution in living *T. adriatica* and records of rare occurrences of fossil *Cyclagelosphaera* in Oligocene–Miocene shallow water sediments, from the New Jersey shelf, suggest that *Tergestiella*/*Cyclagelosphaera* was restricted to nearshore environments during much of the Cenozoic. This restricted ecology explains the lack of fossil *Tergestiella*/*Cyclagelosphaera* recorded in open ocean sediments deposited during the last 54 myr.
Floristic study of coccolithophores in the coastal and offshore waters of Tomari over a six-year period, show that *T. adriatica* occurs synchronously with the unusual neritic species, *Braarudosphaera bigelowii*, in mid-June. The environmental factors that induce the co-occurrence of these two taxa are uncertain, and *T. adriatica* did not co-occur with *B. bigelowii* at any other sites.

1. Introduction

Coccolithophores are mostly marine unicellular haptophytes characterized by calcareous scales called coccoliths (e.g., Young et al., 2003). Fossil coccoliths and other calcareous microfossils of uncertain affinities are collectively referred to as calcareous nannofossils (Bown, 1998). Calcareous nannofossils, which appeared in the late Triassic (~225 Ma), progressively diversified through the Jurassic and Cretaceous periods, despite some extinction and turnover events. The highest diversity of calcareous nannofossils is recorded in the Campanian and Maastrichtian (80–68 Ma); however, 85% of genera and 93% of species went extinct at the K/Pg (Cretaceous/Paleogene) mass extinction event at 66 Ma (Bown et al., 2004). Immediately after the extinction, a low diversity assemblage of coccolithophore survivor species flourished, followed by a rapid evolutionary radiation of new Cenozoic taxa (e.g., MacLeod et al., 1997). Most K/Pg survivors went extinct in the Cenozoic; however, three K/Pg survivor taxa are known to be extant: *Braarudosphaera*, *Calciosolenia*, and *Cruciplacolithus* (Young et al., 2003; Bown, 2005).

During studies of living *Braarudosphaera* in the coastal-offshore waters of Tomari Port, Tottori, Japan (western Sea of Japan) (Hagino et al., 2013), we encountered coccolithophore specimens with distinctive circular coccoliths, which were unlike any we had previously seen in the plankton but which were essentially identical to the supposedly extinct Mesozoic genus *Cyclagelosphaera*. This suggested the possibility that it might be a remarkable new example of a living fossil. Indeed, as *Cyclagelosphaera* first occurred in the Middle Jurassic (ca. 170 Ma; Bown and Cooper, 1998) this would make it the oldest extant coccolithophore genus. Subsequently, we found similar specimens in offshore seawater samples from Rovinj, Croatia (north Adriatic Sea). As described below, re-examination of the classic literature revealed that Kamptner (1940) described this species as *Tergestiella adriatica* from the northern Adriatic Sea, although it has not been reported

* Corresponding author at: Research and Education Faculty, Natural Sciences Cluster, Sciences Unit, Kochi University, Akebono-cho 2-5-1, Kochi 780-8520, Japan. Tel.: +81 858 43 3827.
E-mail address: hagino@kochi-u.ac.jp (K. Hagino).

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in 70 years of subsequent studies, and was not known to current researchers.

To determine the phylogenetic affinities of *Tergestiella* to *Cyclagelosphaera*, we conducted detailed morphological studies of the specimens from both Tomari and Rovinj using the scanning electron microscope (SEM) and cross-polarized light microscope (LM). We also carried out molecular phylogenetic studies based on 18S rDNA sequences obtained from the specimens from Tomari to test whether *Tergestiella* was closely related to any of the well-known extant coccolithophore groups, or deeply diverged from them, as would be expected if it is a descendent of the Mesozoic *Cyclagelosphaera*. Also, we studied the seasonal succession of living coccolithophores, including *T. adriatica*, from the coastal and offshore waters of Tomari in order to determine their ecological preferences. Furthermore, we re-examined fossil specimens of '*Cyclagelosphaera*?' reported from Oligocene–Miocene sediments of the New Jersey margin (Mountain et al., 2010) under the LM.

2. Materials and methods

2.1. Sampling

Sea-surface water samples (10–12 L) were collected by bucket from the quay or breakwaters of Tomari Port (stations Tomari 1, A, B, C, D, and/or E) and from the breakwater of Ishiwaki (station Ishiwaki) on 167 occasions from July 2008 to June 2014 (Fig. 1, Appendix 1). 65 sea-surface water samples from offshore Tomari were collected from the fishing boat (*Ryoto-Maru*) using a 10 L plastic bottle, from July 2007 to July 2013 (Appendix 1). The offshore sampling water depth was measured by a fish-detector and ranged from 20–50 m. The sampling interval was adjusted according to the season, from July 2008 to March 2012 (Supplementary materials).

Samples from offshore Rovinj (Croatia), were collected once or twice a month from August 2009 to 2010, as a supplement to a regular time-series sampling program conducted by the Centre for Marine Research

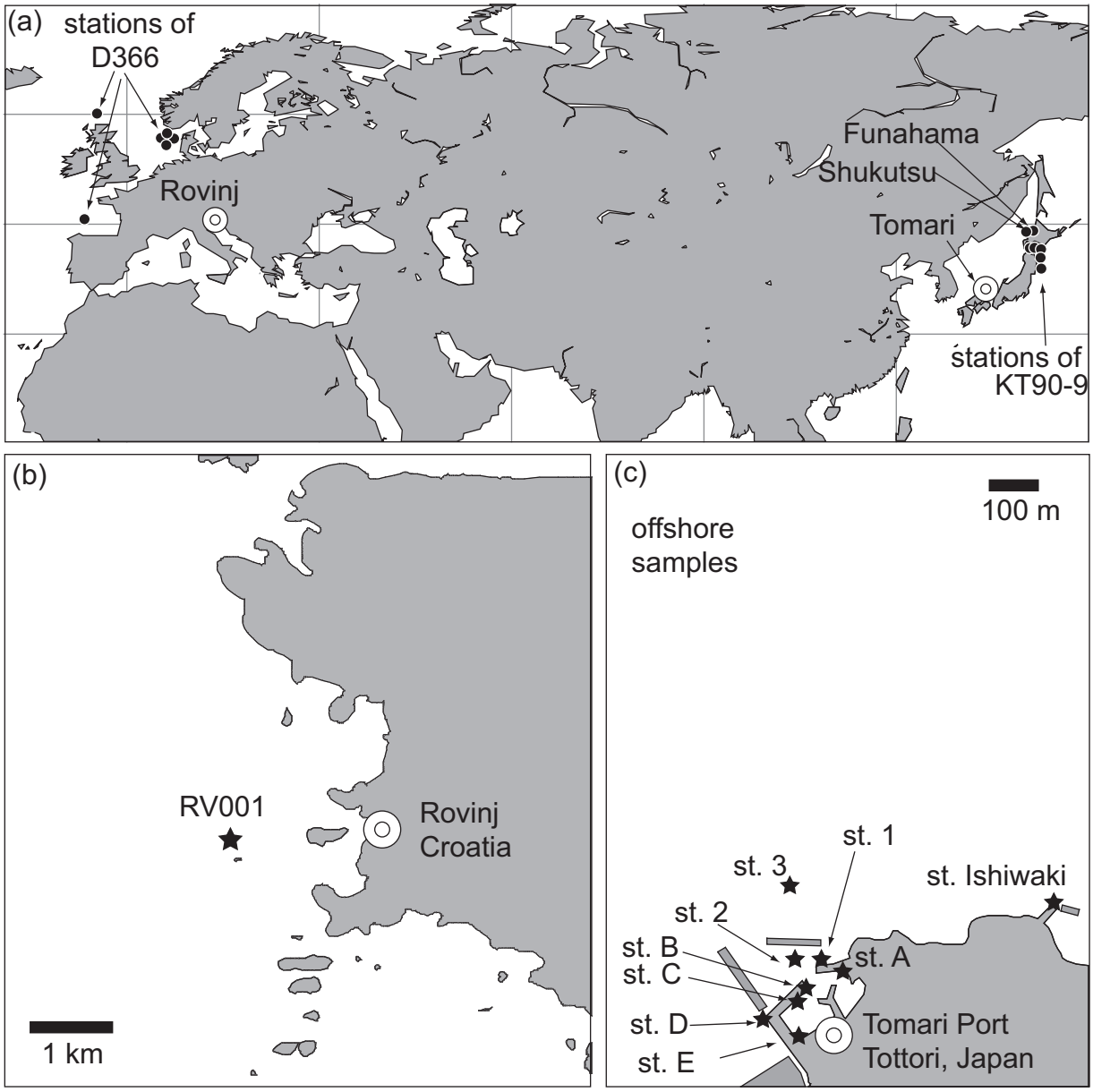

Fig. 1. Location of samples used in this study: (a) double white circles show the bases used for repeated sampling in this study, and solid black circles show the locality of samples containing *Braarudosphaera* that were re-examined in this study. (b) Locality of samples offshore Rovinj. (c) Locality of samples of coastal and offshore Tomari Port.