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Research paper

Combination coccospheres from the Eastern Adriatic coast: New, verified and possible life-cycle associations

Luka Šupraha[a,*,1], Zrinka Ljubešić[b], Jorijntje Henderiks[a,c]

[a] Paleobiology, Department of Earth Sciences, Uppsala University, Villavägen 16, Uppsala SE-752 36, Sweden
[b] Department of Biology, Faculty of Science, University of Zagreb, Rooseveltov trg 6, Zagreb 10000, Croatia
[c] CEES, Department of Biosciences, University of Oslo, P.O. Box 1066, Blindern, Oslo 0316, Norway

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ABSTRACT

Coccolithophore life cycles involve the alternation between morphologically distinct life-cycle phases. This often leads to taxonomic issues where the life-cycle phases of the same species are described as distinct taxa. This issue can be resolved by the observation of combination coccospheres, *i.e.* cells bearing the coccoliths of both life-cycle phases. This study presents new observations on combination coccospheres from the highly diverse and ecologically important coccolithophore order Syracosphaerales and the genus *Alisphaera*. New life-cycle associations are revealed between *Syracosphaera hirsuta* and *Corisphaera strigilis*, and between *Alisphaera unicornis* and a nannolith-producing *Polycrater galapagensis*. The life-cycle association of *Syracosphaera marginiporata* – *Anthosphaera* sp. type B is verified. A possible association between *Rhabdosphaera xiphos* and an unidentified holococcolith-bearing morphotype is proposed and needs to be verified in future investigations. The appropriate taxonomic revisions are conducted following the taxonomic principle of priority and recommended practices for naming the coccolithophore life-cycle phases.

1. Introduction

Coccolithophores (division Haptophyta) are an ecologically and biogeochemically important group of microalgae (Rousseaux and Gregg, 2013) which cover their cells with tiny calcite plates called coccoliths (Westbroek et al., 1984). A majority of modern coccolithophore species exhibit a heteromorphic life cycle (Young et al., 2005), alternating between two functionally (Houdan et al., 2006) and morphologically distinct life-cycle phases (Nöel et al., 2004). These species typically cover their diploid cells with intracellularly produced heterococcoliths (plates made of radially arranged crystalline units) and their haploid cells either with extracellularly produced holococcoliths (plates made of tiny rhombohedral crystallites) (Houdan et al., 2004) or nannoliths (Cros and Fortuño, 2002; Young et al., 1997).

The heteromorphic nature of the coccolithophore life cycle has led to taxonomic issues, as life-cycle phases of the same species have often been described as separate species. A key way of uniting separate hetero- and holococcolith-bearing morphospecies into a single life cycle is through field observations of combination coccospheres (Cros et al., 2000; Thomsen et al., 1991; Triantaphyllou et al., 2016). These specimens represent the cells observed after the transition between the two life-cycle phases and are covered with both heterococcoliths and holococcoliths or nannoliths, allowing for the reconstruction of the life-cycle and synonymization of previously separate taxa.

This study presents new findings of combination coccospheres belonging to species from the highly diverse order Syracosphaerales and the genus *Alisphaera* observed during an investigation of coccolithophore life-cycle dynamics in the Eastern Adriatic Sea (Mediterranean Sea) (Šupraha et al., 2016; Šupraha et al., 2014). Two new combinations are reported: *Syracosphaera hirsuta* Kleijne & Cros - *Corisphaera strigilis* Gaarder and *Alisphaera unicornis* Okada & McIntyre - *Polycrater galapagensis* Manton & Oates. The combination between *Syracosphaera marginiporata* Knappertsbusch – *Anthosphaera* sp. type B as proposed by Cros and Fortuño (2002) is verified herein and a new combination is proposed between *Rhabdosphaera xiphos* (Deflandre & Fert) Norris and a previously undescribed holococcolith-bearing morphotype. The results contribute to resolving taxonomic issues related to coccolithophore life cycle and provide a basis for future taxonomical, ecological and evolutionary studies.

* Corresponding author.
E-mail address: luka.supraha@ibv.iuo.no (L. Šupraha).
[1] Present address: Section for Aquatic Biology and Toxicology (AQUA), Department of Biosciences, University of Oslo, Oslo 0316, Norway.

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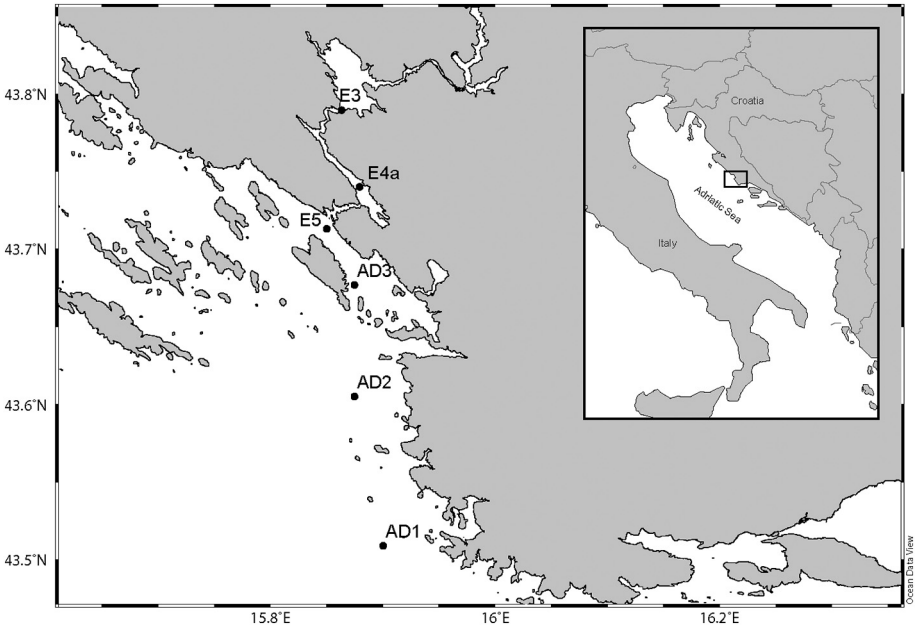

Fig. 1. Map showing the locations of sampling sites within the Krka River Estuary (E3-E5) and at the Eastern Adriatic coast (AD1-AD3).

2. Material and methods

A total of 63 samples were collected in winter (February) and summer (July) 2013, at six stations located along a deep-to-shallow transect, from the coastal Eastern Adriatic Sea (stations AD1, AD2 and AD3) to the lower reach of the Krka River Estuary (stations E5, E4a and E3) (Fig. 1, Table 1). Seawater was obtained using a series of 5 L Niskin samplers. For the quantitative and qualitative analysis, a known volume of seawater was filtered onto a 25 mm polycarbonate filter (0.8 µm Cyclopore, Whatman) using a weak vacuum. A 25 mm cellulose nitrate filter (Whatman) of the same diameter and pore size was placed underneath the polycarbonate filter to obtain the even distribution of the filtered material. The material was then rinsed with 2 mL of a bottled drinking water (pH = 7.54) and dried in an oven at 50 °C. Finally, a piece of filter was mounted on a metal stub, sputter-coated with gold for 80 s and analysed under a Zeiss Supra35-VP scanning electron microscope (SEM).

The quantitative analysis of coccolithophore assemblages was conducted following Bollmann et al. (2002) (detailed description of the methodology is provided by Šupraha et al. (2016)). All observed specimens were identified to the lowest possible taxonomic level using the standard taxonomic literature (Cros and Fortuño, 2002; Young et al., 2003). Detailed morphological descriptions followed the terminology provided by Young et al. (1997) as well as terminology used in the studies on Rhabdosphaeraceae by Kleijne (1992), Alisphaeraceae (Kleijne et al., 2001) and Syracosphaeraceae (Kleijne and Cros, 2009). Taxonomical revisions followed the principle of priority as established by the International Code of Nomenclature (McNeill et al., 2012) as well as the recommendations given by Cros et al. (2000) for the cases in which the holococcolith-bearing phase has the taxonomic priority.

Table 1
List of sampling stations with coordinates and sampled depths.

Station	Latitude (N)	Longitude (E)	Season	Date	Depths (m)
AD1	43.5088	15.9003	Winter	25.2.2013	0, 10, 25, 40, 60, 90
			Summer	8.7.2013	0, 10, 40, 50, 60, 90
AD2	43.6051	15.8753	Winter	25.2.2013	0, 10, 25, 42, 60, 70
			Summer	8.7.2013	0, 15, 25, 40, 48, 60
AD3	43.6768	15.8742	Winter	25.2.2013	0, 10, 30, 45
			Summer	8.7.2013	0, 10, 30, 40
E5	43.7129	15.8502	Winter	25.2.2013	0, 3, 10, 35
			Summer	8.7.2013	0, 3, 10, 35
E4a	43.7392	15.8805	Winter	25.2.2013	0, 3, 5, 20, 35
			Summer	8.7.2013	0, 1.5, 3, 5, 20, 30
E3	43.7898	15.8633	Winter	26.2.2013	0, 4, 5, 7.5, 13, 20
			Summer	8.7.2013	0, 2.5, 3, 3.5, 5, 15

3. Results and discussion

The study of coccolithophore life-cycle dynamics in the Eastern Adriatic coast and the Krka River estuary detected a total of 111 coccolithophore morphotypes belonging to 82 coccolithophore species (Šupraha et al., 2016). The same study found 11 combination coccospheres, 7 of which were previously described (Šupraha et al., 2016). The remaining four combination coccospheres represent new findings and are presented here.

3.1. *Syracosphaera hirsuta* (Kleijne and Cros, 2009) – *Corisphaera strigilis* (Gaarder, 1962)

Three specimens of this combination coccosphere were observed (Fig. 2b–d), confirming the life-cycle phase association between the two morphospecies. All specimens were found during the winter sampling, both at the coastal stations (surface of AD1 and at 10 m depth at AD3) and within the Krka River estuary (3 m depth at E4a). The heterococcolith-bearing phase (Fig. 2a) was found in 58% of winter samples, reaching the highest abundance (4.03×10^3 cells L^{-1}) at 3 m depth at station E5, but was rare during summer (6% of samples). On the other hand, the holococcolith-bearing phase (Fig. 2e) was rare during winter (6% of samples) and more common during summer (22% of samples) with a peak abundance observed at 25 m depth at AD2 (2.01×10^3 cells L^{-1}). Both life-cycle phases preferred the coastal stations (AD1-E5) and were rare within the estuary.

All of the observed combination coccospheres were collapsed and shared a similar morphology, having one half of the coccosphere covered with ~4–12 *S. hirsuta* heterococcoliths and another half with ~42–73 holococcoliths of *C. strigilis*. The heterococcoliths exhibit

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