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EARLY TRIASSIC ORIGIN OF COCCOLITHOGENESIS

ELISABETTA ERBA[1], CINZIA BOTTINI[1*], DA-YONG JIANG[2], RYOSUKE MOTANI[3], ANDREA TINTORI[1] & GIULIA FAUCHER[4]

[1]Department of Earth Sciences, Università degli Studi di Milano, 20133 Milan, Italy. E-mail: cinzia.bottini@unimi.it
[2]Laboratory of Orogenic Belt and Crustal Evolution, Ministry of Education; Department of Geology and Geological Museum, Peking University, Yiheyuan Street. 5, Beijing 100871, People's Republic of China
[3]Department of Geology University of California DAVIS, California 95616, USA.
[4]Biological Oceanography, GEOMAR Helmholtz Centre for Ocean Research Kiel, 24148 Kiel, Germany.
*Corresponding Authors.

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Keywords: calcareous nannofossils; Early Triassic; coccolithogenesis; South China.

Abstract: Calcareous nannofossil investigations were conducted on Lower and Middle Triassic marine successions from South China. Coccoliths, nannoliths and calcispheres are relatively frequent and moderately preserved, showing an increase in diversity from the Smithian (Olenekian) to the Ladinian. The oldest nannofossils, dated to the Smithian, include *Eoconusphaera hallstattensis* and very simple coccoliths attributed to a sp. A morphogroup. Nannoliths of *Prinsiosphaera triassica* and *Carnicalyxia*, along with rare specimens of *Tetralithus pseudotrifidus* and *Crucirhabdus* cf. *C. minutus* are present in the Spathian-Pelsonian (Olenekian-Anisian) and Longobardian (Ladinian) samples, respectively. A total of 10 new morphotypes are also described. The Smithian coccoliths documented here significantly narrow the temporal gap between molecular clock estimates for the origin of calcifying coccolithophores and their first fossil record. Our data represent the oldest known nannofossils and push back the onset of coccolithophore calcification by approximately 40 million years, shortly after the end-Permian mass extinction. The Olenekian primitive, simple and tiny coccoliths from South China suggest that early coccolithophores emerged in a coastal environment of the eastern Tethys Ocean. The onset of calcification in Calcihaptophycidae may have been facilitated by suppressed atmospheric CO_2 levels, coupled with increased nutrient availability following the emplacement of the Siberian Traps. The emergence of this new phytoplanktonic group correlates with the earliest recovery of benthic calcifiers, potentially shaping post-extinction marine biodiversity and influencing the evolution of the ocean toward modern conditions.

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INTRODUCTION

Coccolithophores, golden-brown algae with red "plastids" (chlorophyll c as an accessory pigment) of Phylum Haptophyta, secrete submicroscopic low-Mg calcite crystals to construct coccoliths adjusted into an exoskeleton, named coccosphere, around the cell (Lohman 1902). Along with diatoms, phytoplanktonic cyanobacteria and dinoflagellates, coccolithophores are a foremost constituent of the marine functional groups responsible for primary productivity, energy transfer to higher trophic levels, export of biogenic particles to the seafloor and exchanges with the atmosphere. Coccolithophore biomineralization converts Ca and inorganic C (bicarbonate ions) into calcite at very fast (days to weeks) reproduction rates, making this phytoplanktonic group most effective calcite producers on Earth since Mesozoic times (Bown et al. 2004; Erba & Tremolada 2004; Erba, 2006; Suchéras-Marx et al. 2019). Living coccolithophores can secrete both coccoliths and nannoliths (Young et al. 1999) that are consistently found in various proportions in Recent to Jurassic sedimentary sections. Coccolith, nannolith and coccosphere accumulation on the seafloor is a large long-term C sink that contributes to the vertical CO_2 gradients in the ocean on geological time scales. Arguably, the invention of coccolith calcification by the Subclass Calcihaptophycidae (De Vargas et al. 2007*)* must be regarded as a fundamental step towards the modern ocean.

While molecular studies on coccolithophores are crucial for reconstructing their biological origin and evolution, micropaleontological investigations - although undoubtedly incomplete relative to living coccolithophore populations (Bown et al. 2004) - remain the only direct way to date coccolithogenesis origin and development. Specifically, the most ancient coccolith unequivocally dates the initial secretion of calcite liths above organic baseplates (Young & Henriksen 2003). The oldest record of calcareous nannofossils consists of nannoliths and calcispheres dated as Carnian (Late Triassic) followed by coccoliths in the Norian (Bown 1998). These relatively common nannofossils indicate that biological processes analogous to those operating today were already in place in Late Triassic times *(*Young et al. 1999; Bown et al. 2004; Young & Henriksen 2003; Falkowski et al. 2004*)*. Based on revised stratigraphy (Gardin et al. 2012), the oldest nannoliths are documented in Carnian layers, while the oldest coccoliths occur in uppermost Norian sediments from the Austrian Alps, suggesting that perhaps the Western Tethys was the birthplace of coccolithophores. Demangel et al. (2020, 2023) confirmed the first occurrence of the coccolith species *Crucirhabdus minutus* and *Archaeozygodiscus koessenensis* in the upper Norian interval of the Northern Calcareous Alps (Austria), although unspecified coccoliths – not determined at the species level – were observed in middle Norian samples. After the appearance in the Carnian, according to Demangel et al. (2023) *Prinsiosphaera triassica* became rock-forming in the upper Rhaethian as documented in the Northern Calcareous Alps. Bottini et al. (2016) documented calcareous nannofossils in the Rhaethian of the Southern Alps. Findings of Upper Triassic calcareous nannofossils from areas outside the Tethyan Realm are limited to the Wombat Plateau, north-western Australia (Bralower et al. 1991, 1992), the Queen Charlotte Islands, western Canada (Bown 1992), the Neuquén Basin in west-central Argentina (Pérez Panera et al. 2023a) and the East Andes in northern Peru (Pérez Panera et al. 2023b).

The study of Lower and Middle Triassic samples from South China provides evidence of the potential occurrence of calcareous nannofossils in earliest Mesozoic, constraining the beginning of coccolithogenesis and documenting nannofloral diversity through the Triassic.

STRATIGRAPHIC SETTING

In South China marine sequences of Early-Middle Triassic age revealed the occurrence of extremely diversified and well-preserved marine faunas, including reptiles, fishes, conodonts, daonellid bivalves, and ammonoids (Motani et al. 2008; Jiang et al. 2005, 2009, 2016; Sun et al. 2013; Tintori et al. 2014; Zou et al. 2015*)*. The South China Lower and Middle Triassic marine sequence was, therefore, thoroughly studied in the past few decades, because of such exceptional paleontological records preserved in many Lagerstätten intervals, as reviewed by Benton et al. (2013). The Lower Triassic sequence exposed at Pingdingshan-Majiashan in Chaohu, Anhui Province is a complete Induan and Olenekian succession deposited in a relatively deep-water slope setting (200 to 500 m) on the northern border of the

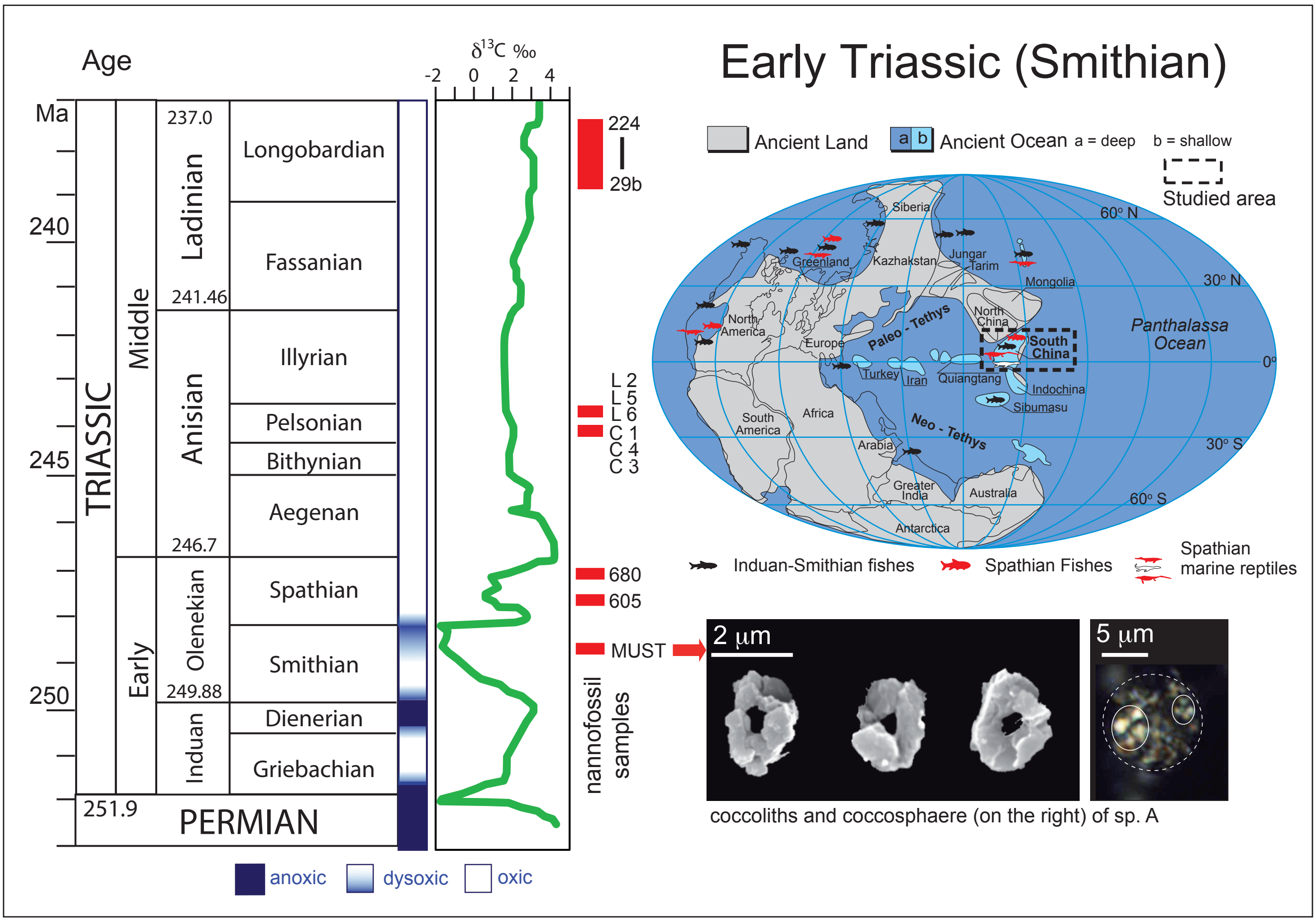

Fig. 1 - Left: Stratigraphic framework for the Early-Middle Triassic with the samples investigated for calcareous nannofossils. Right: at the top a Smithian paleogeographic reconstruction with indication of the studied area. Spathian marine reptiles: A = Endemic Ichthyosauriformes genera (*Grippia-Parvinatator-Utatsusaurus-Gulosaurus*); B = Eosauropterygia (*Majiashanosaurus*); C = Ichthyosauromorpha (Hupehsuchia + Nasorostra + *Chaohusaurus*). In the lower part: photos of the oldest coccoliths found in the Smithian sample.

Yangtze Platform connecting the eastern Tethys and western Panthalassa oceans (Tong & Yin 2002; Sun et al. 2009; Tong & Zhao 2011) (Fig. 1).

The basal Triassic Yingkeng Formation, overlying the Permian Dalong Formation and overlaid by the Helongshan Formation, is composed of black shales, light grey, green, yellowish mudstones and shales intercalated with thin-bedded muddy limestones and nodular limestones. The Induan/Olenekian boundary was proposed to be at the base of Bed 24-16 of the Pingshan section, defined by the first appearance of conodont *Neospathodus waageni* (Tong & Zhao 2011).

The Smithian Helongshan Formation is well exposed at Majiashan and represents a highly cyclic sedimentation of alternating pyrite-rich marlstones and bivalve wackestones. It is subdivided into two members. The Lower Member comprises yellowish grey-purple, thin-bedded, nodular limestones, calcareous mudstones, and light grey, medium-bedded, muddy limestones. The Upper Member mainly consists of grey thin-bedded limestones intercalated with yellowish-green, thin-bedded, nodular limestones. The uppermost beds are black shales and dark grey, thin-bedded marlstones, yielding nodules (calcareous concretions) containing abundant fishes, ammonoids and bivalves. The Smithian/Spathian boundary, defined by the first appearance of conodont *Neospathodus pingdingshanensis* is in the uppermost part of the Helongshan Formation (Liang et al. 2011).

The Lower Qinglong Formation - comprising alternating thin-bedded muddy limestones, calcareous mudstones and limestones - is equivalent to both the Yinkeng Formation (Griesbachian to early Smithian) and Helongshan Formation (late Smithian) at Chaohu (Chen et al. 2011; Benton et al. 2013).

The Spathian Nanlinghu Formation is subdivided into three members. The Lower Member is characterized by light grey, thick-bedded limestones.

The Middle Member consists of reddish, medium-thick-bedded, nodular limestones. The Upper Member consists of dark grey, thin-bedded marlstones and muddy limestones intercalated with yellowish green calcareous shells (lower part), and dark grey to black, thin-bedded marlstones and limestones intercalated with bituminous shells and carbonaceous shells (upper part).

The Anisian Guanling Formation mainly comprises clastic rocks and carbonates. The Lower Member contains yellow-green fine sandstones, silty mudstones and mudstones intercalated with muddy dolomites interpreted to reflect a transition from restricted-evaporitic tidal flat to shallow marine facies, whereas the Upper Member comprises light-grey to dark-grey, nodular micritic limestones, muddy limestones and cherty micritic limestones with bands of dolomites.

The Illyrian-Fassanian (Anisian-Ladinian) Yangliujing Formation corresponds to 'the Member III of the Guanling Formation' of Zhang et al. (2009). It is strongly dolomitized and interpreted as the Ladinian evaporative tidal sediments that comprises medium- to thick-bedded dolostones or calcite dolostones intercalated with pseudomorphs of gypsum- and evaporate-solution breccias.

The Longobardian Zhuganpo Member of the Falang Formation is well exposed near the village of Nimaigu (Wusha District) and consists of dark-grey to grey, medium-bedded, micritic limestones, nodular limestones and argillaceous layers. It is dated as late Ladinian based on ammonoids (Zou et al. 2015) and conodonts (Sun et al. 2016). Radiometric dating based on zircon U-Pb was achieved for tuff at the bottom of Layer 47, providing an age of 240.8 ± 1.8 Ma (Lu et al. 2018).

Samples and Methods

Calcareous nannofossils were analysed in samples from the Longtan, Majiashan, Luoping and Nimaigu sections (Fig. 2) previously investigated for marine faunas and available at the Department of Earth Sciences of the University of Milan (Italy). The study was conducted on limy and marly beds of the Quinglong Formation (Smithian) at Longtan (Anhui Province), the Nanlinghu Formation (Spathian) at Majiashan (Anhui Province), the Upper Member of the Guanling Formation (Pelsonian) at Luoping (Yunnan Province) and the Zhuganpo Member of the Falang Formation (Longobardian) at Nimaigu (Wusha District, Guizhou Province) (Figs. 1 and 2). Specifically:

a) Nannofossil MAST sample derives from a fish-bearing nodule collected from the upper part of the Lower Qinglong Formation at Longtan. The detailed lithostratigraphy of the Longtan section is described by Liu et al. (2020) who performed a high-resolution conodont biostratigraphy providing a latest Smithian age.

b) Nannofossil samples 605 and 680 are from the Middle Member and Upper Member, respectively, of the Nanlinghu Formation outcropping at Majiashan (Motani et al. 2015). Based on ammonoid biostratigraphy a middle Spathian age was derived (Ji et al. 2015).

c) Nannofossil samples C1, C3 and C4 were taken from the Panxian Level and samples L2, L5 and L6 are from the Luoping Level in the Upper Guanling Formation outcropping at Luoping. A Pelsonian age is based on conodonts and ammonoids (Zhang et al. 2009).

d) Nannofossil samples 29b to 224 were collected from the Nimaigu section. The investigated interval was dated as late Ladinian (Longobardian) based on ammonoids (Zou et al. 2015) and conodonts (Sun et al. 2016).

Calcareous nannofossils were investigated in smears slides by light polarizing microscope at 1250X magnification. Smear slides were prepared using the standard technique (Monechi & Thierstein 1985), without centrifuging cleaning/concentration in order to retain the original sediment composition. A small quantity of rock was powdered in a mortar with bidistillate water and mounted on a glass slide with Norland Optical Adhesive. A total of 23 samples were investigated through analyses of 2 smear slides/sample for a total of 160 traverses (24000 fields of view) for each sample. In addition, samples MAST, 680, C1, L6, 35, 41 and 224 were also analyzed under Scanning Electron Microscope (SEM) Cambridge S-360 at the University of Milan.

Results

Coccoliths, nannoliths and calcispheres were observed in 22 out of 23 samples (Fig. 3): in general, marlstones yield relatively richer assemblages with

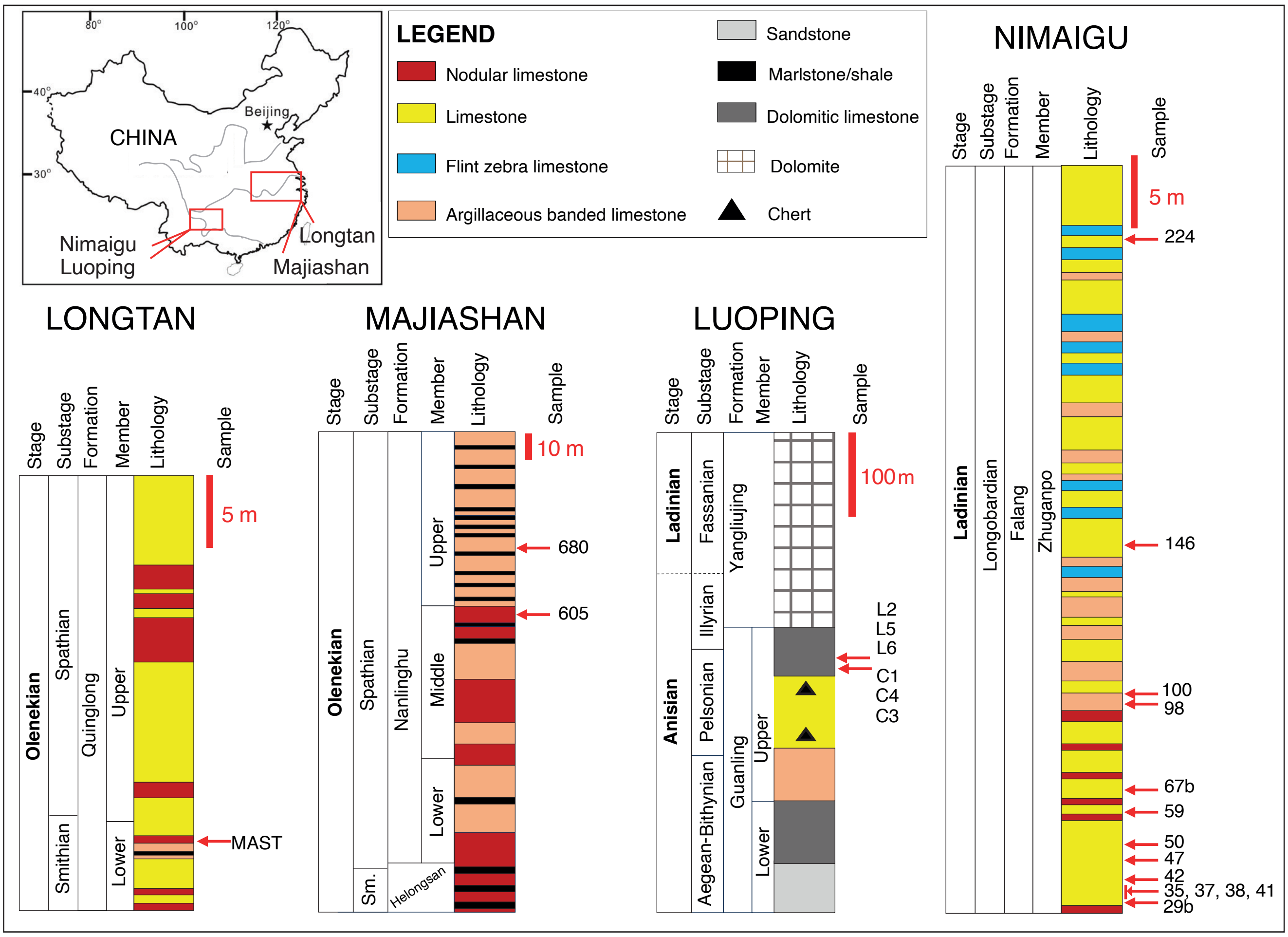

Fig. 2 - Simplified litho-chronostratigraphy of the sections sampled for nannofossil investigations. The Longtan section is modified after Liu et al. (2020), the Majiashan section is modified after Jiang et al. (2016), the Luoping section is modified after Sun et al. (2016) and the Nimaigu section is modified after Zou et al. (2015).

more abundant tiny coccoliths, whereas limy lithologies are enriched in nannoliths and calcispheres. Calcareous nannofossil preservation is generally moderate and diversity increases upwards: both coccoliths and nannoliths, although with low abundance, are present in the lowermost sample (Smithian). Some of the observed taxa are attributable to species or morphotypes previously documented in Upper Triassic sequences (Figs. 3 and 4), but most coccoliths and nannoliths found in South China have not been recorded before. Among the established Triassic nannofossil taxa, we observed *Eoconusphaera hallstattensis*, *Carnicalyxia* sp., and *Prinsiosphaera triassica* (small and large forms). Plates 1-3 illustrate the Early-Middle Triassic nannofossil taxa and morphotypes identified in this study; the taxonomy is detailed in the Appendix I.

The Smithian lowermost sample contains *E. hallstattensis* and very simple coccoliths (sp. A) (Figs. 1 and 3). Other coccoliths and nannoliths were detected in the Spathian samples and an increase in diversity continues in the Anisian reaching a total of 16 forms in the Ladinian (Figs. 3 and 4). In Spathian and Pelsonian samples nannoliths of *P. triassica* and *Carnicalyxia* were also observed. Rare specimens of *Tetralithus pseudotrifidus* and *Crucirhabdus* cf. *C. minutus* are present in the Ladinian interval (Fig. 3).

The small size (2-2.5 µm) and simple structure of sp. A coccoliths observed in the Smithian sample are compatible with early primitive liths. They are consistently present through the studied interval and a few coccospheres were observed from the Smithian sample upwards, thus indicating that coccolithogenesis was already operating in the Early Triassic, some 249 Ma. The sp. A coccoliths do not resemble any specimens previously documented from the Upper Triassic, while the sp. D coccoliths are similar to undetermined specimens described from the Northern (Gardin et al. 2012*)* and Southern (Bottini et al. 2016) Alps (Fig. 4).

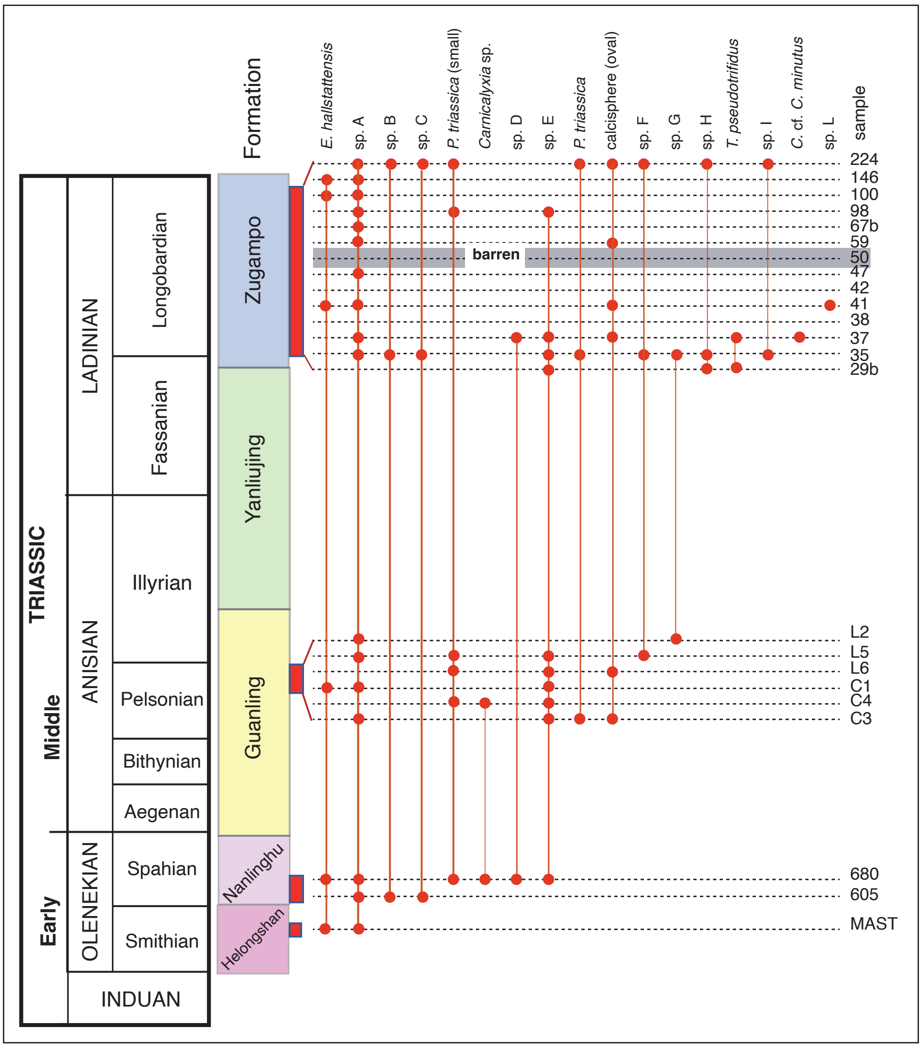

Fig. 3 - Occurrences of coccolith/nannolith taxa and morphotypes in Lower and Middle Triassic samples from South China. Taxonomic remarks in Appendix I.

Our findings document the oldest coccoliths found to date and bring the minimum age of coccolithophorid calcification back by ~40 million years. Although this discovery is based on only one area, we deduce that the production, deposition and preservation of phytoplankton carbonate - at least in a coastal location of an open ocean environment - began already in Early Triassic times. The relatively diversified assemblages found in the Olenekian samples of South China presumably imply an even older origination of coccolith/nannolith-bearing coccolithophores. However, older Triassic nannofossils have not been documented so far and Paleozoic coccolith-like objects (Deflandre 1970; Pirini Radrizzani 1971; Gartner & Gentile 1972) remain highly debated and considered unlikely to be coccolithophore liths (Young et al. 2025). De Vargas et al. (2007) discuss the possibility that calcifying coccolithophores originated in the Late Permian (Fig. 4). However, they possibly were extremely rare and problematic to be preserved in the fossil record.

The Triassic evolution of coccolithogenesis remains difficult to reconstruct because the new data are essentially detached from the described Upper Triassic nannofossils (Bellanca et al. 1993; Gardin et al. 2012; Bottini et al. 2016; Demangel et al. 2020, 2023; Pérez Panera et al. 2023a, 2023b) and there are no studies documenting calcareous nannofloras in Lower and Middle Triassic sequences. However, sp. D coccoliths are comparable to the Norian unknown coccoliths reported from the Northern Calcareous Alps by Gardin et al. (2012*)* and the Rhaetian sp. 5 specimens described from the Southern Alps by Bottini et al. (2016). A few specimens of *T. pseudotrifidus* analogous to those reported from the Rhaethian (Bottini et al. 2016) and rare coccoliths similar to *C. minutus* are present in the Ladinian assemblages of South China. The Late Triassic coccolith species *Archaeozygodiscus koessenensis* and *Crucirhabdus primulus*, instead, were not found in the analyzed South China samples, suggesting that their origin is younger than Ladinian times.

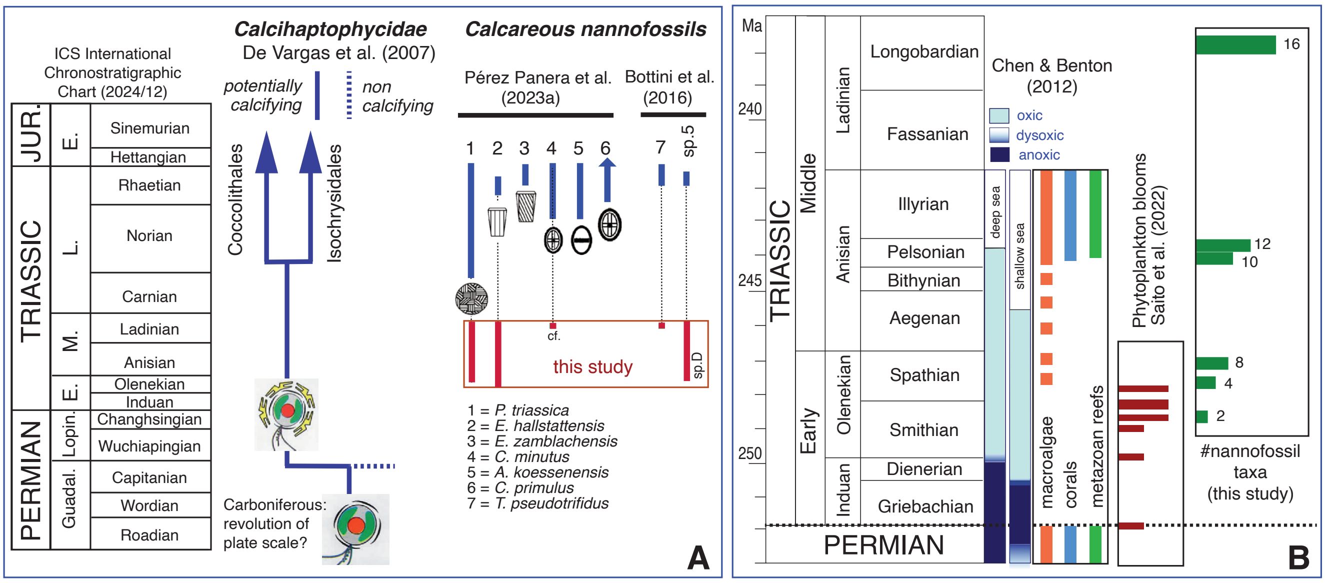

Fig. 4 - A) evolution of Calcihaptophycidae based on molecular clocks and occurrence of calcareous nannofossils in Triassic sequences. B) changes in redox conditions, distribution of calcifying benthic organisms, phytoplankton blooms based on biomarkers and number of nannofossil taxa in the latest Permian to Middle Triassic interval.

Beginning of coccolithogenesis in the Early Triassic and implications for the oceanic ecosystem

The rise of coccolithogenesis is one of the most profound ecological innovations in the oceanic ecosystem and Lower Triassic calcareous nannofossils from South China provide a chance to examine the circumstances that prompted (or allowed) a group of phytoplankton to mineralize calcite, in fact dating the birth of the modern ocean. Smithian nannofossils found in South China significantly reduce time discrepancy between origin of coccolithophores based on molecular clocks and fossil record (De Vargas et al. 2007). Molecular-based phylogenetic reconstructions predict a Triassic age for the origin of calcifying Haptophytes, following the Permian splitting between the Prymnesiales and the lineage leading to coccolithophores (De Vargas et al. 2004) (Fig. 4). Calcihaptophycidae monophyly advocates that the initiation of coccolithogenesis started after the molecular-based origin of the group and De Vargas et al. (2007) estimated a Late Permian to Middle Triassic age, which is consistent with the presented results.

The oldest nannofossils documented here are coeval with a general initial minor rise in global diversity recorded in Smithian times (Payne et al. 2004) in the aftermath of the catastrophic mass extinction that, at the end of the Permian, imposed a reset of marine ecosystems and forced biota to adapt to, and perhaps take advantage from, extreme climatic and chemical conditions of the ocean fostering novel niches (Sun et al. 2012; Takahashi et al. 2015).

The Permian/Triassic boundary “Strangelove Ocean” (Rampino & Caldeira 2005) experienced prompt and large-scale perturbations of the carbon cycle initiated by the Siberian Traps large igneous province, also triggering widespread anoxia and global warming (Bond & Wignall 2014) along with and a substantial decline in seawater pH (Jurikova et al. 2020). Radiometric ages indicate that most of the Siberian Traps’ emplacement occurred at 250 Ma producing a huge amount of fresh basalts in less than 2 My (Reichow et al. 2009).

Under excess CO_2 concentrations and low carbonate saturation probably the ocean became corrosive (Jurikova et al. 2020) impeding coccolithogenesis or rapidly dissolving primitive calcareous nannofossils (Martin 1995). It is possible that the super-oligotrophic Late Permian ocean preferentially supported cyanobacterial phytoplankton rather than calcareous nannoplankton (Martin 1995). The latest Permian - earliest Triassic extreme oceanic conditions were, thus, favorable for acritarchs and prasinophytes (Twitchett et al. 2001) producing “disaster species” (Tappan 1980) blooms.

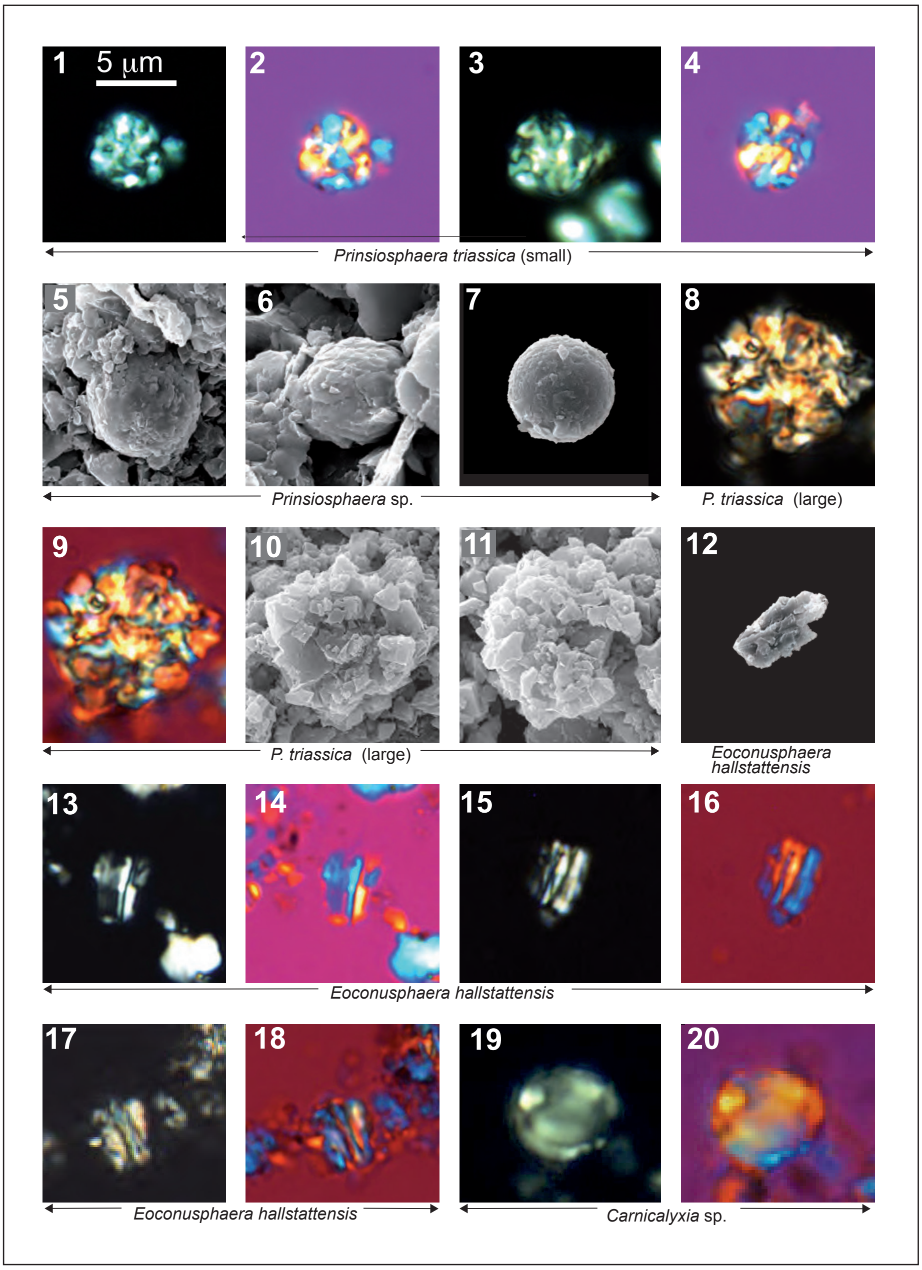

Plate 1

Calcareous nannofossils under light microscope in smear slides (XPL = cross-polarized light; QPL = cross-polarized light with quartz lamina), and under Scanning Electron Microscope. 1) *P. triassica* (small), XPL (sample: L5); 2) *P. triassica* (small), QPL (sample: L5); 3) *P. triassica* (small), XPL (sample: L6); 4) *P. triassica* (small), QPL (sample: L6); 5) *P. triassica* (small), SEM (sample: 224); 6) *P. triassica* (small), SEM (sample: L6); 7) *P. triassica* (small), SEM (sample: C4); 8) *P. triassica* (large), QPL (sample: 224); 9) *P. triassica* (large), SEM (sample: 224); 10) *P. triassica* (large), SEM (sample: 224); 11) *P. triassica* (large), SEM (sample: 35); 12) *E. hallstattensis*, SEM (sample: C1); 13) *E. hallstattensis*, XPL (sample: C1); 14) *E. hallstattensis*, QPL (sample: C1); 15) *E. hallstattensis*, XPL (sample: 41); 16) *E. hallstattensis*, QPL (sample: 41); 17) *E. hallstattensis*, XPL (sample: 41); 18) *E. hallstattensis*, QPL (sample: 41); 19) *Carnicalyxia* sp., XPL (sample: C4); 20) *Carnicalyxia* sp., QPL (sample: C4).

For a few million years in Early Triassic the oceanic system remained disrupted, as evidenced by multiple pronounced carbon isotopic anomalies, and perturbed by pervasive oxygen depletion (Chen & Benton 2012) (Figs. 1 and 4). Anoxic conditions were confined to deep-water settings while coastal environments gradually became oxygenated (Wignall & Twitchett 2002). Persistent anoxia in deep waters and intermittent dysoxia/anoxia in coastal settings – with local photic zone euxinia – were key to N fixation and partitioning of trace elements in the ocean. In coastal environments suboxic to oxic niches were enriched in trace metals such as Mn, Co, Cd through river runoff, while Fe remained soluble in oceanic anoxic waters. Such chemical differentiation possibly regulated the radiation of red algae including coccolithophores in coastal settings (Falkowski et al. 2004). Non-calcifying coccolithophores are typically found in modern littoral environments (De Vargas et al. 2007), although non-mineralized and/or naked groups might also live, without our knowledge, in the open ocean (De Vargas et al. 2004). Biological and phylogenetic information, likewise, suggests that Haptophytes have evolved from coastal or neritic heterotrophs/mixotrophs to oceanic autotrophs since their origination in the Proterozoic (De Vargas et al. 2007). Thus, the red-lineage ancestors of coccolithophores might have taken advantage of coastal habitats that were less affected by, or rapidly recovered from, anoxia

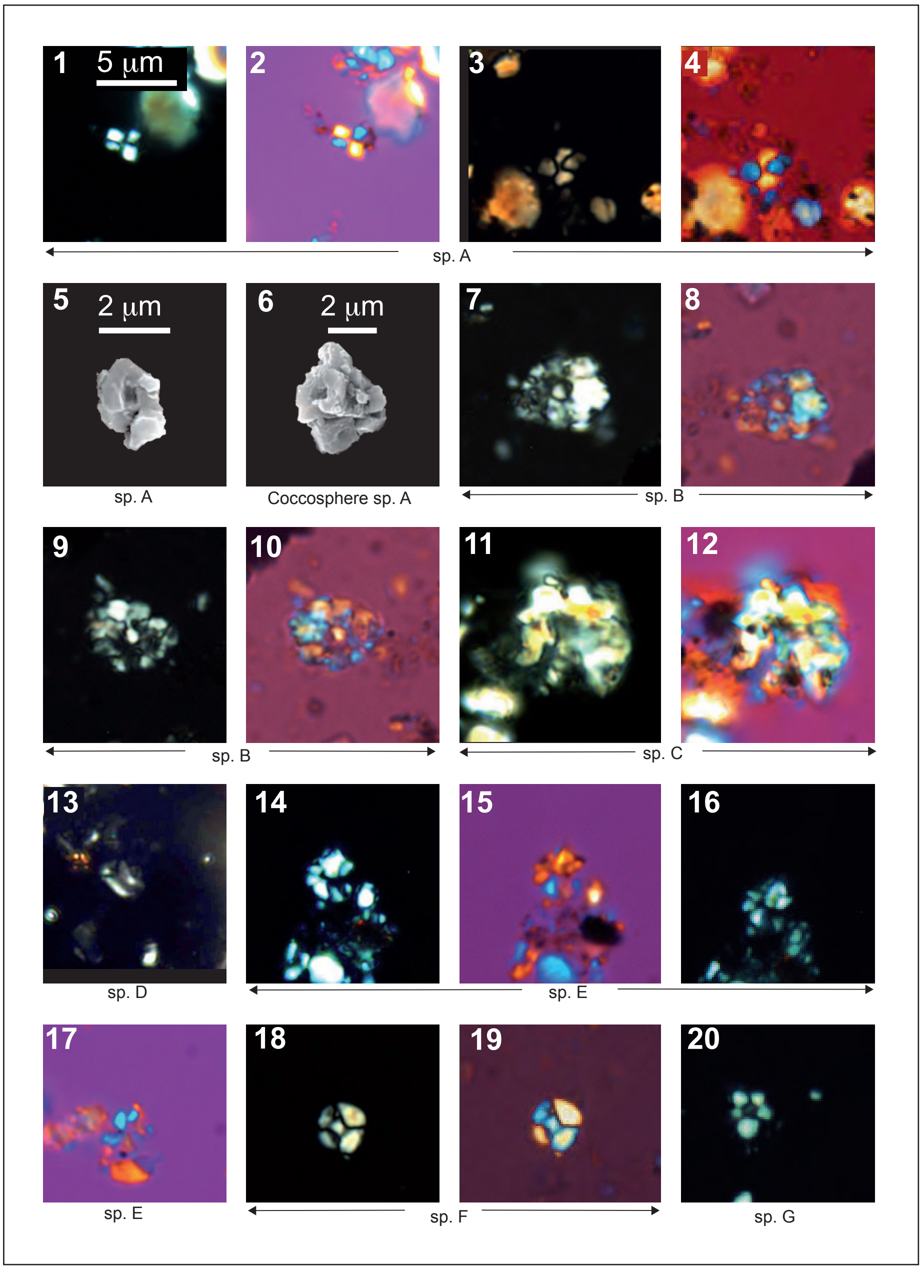

Plate 2

Calcareous nannofossils under light microscope in smear slides (XPL = cross-polarized light; QPL = cross-polarized light with quartz lamina), and under Scanning Electron Microscope (SEM). 1) sp. A, XPL (sample: L2); 2) sp. A, QPL (sample: L2); 3) sp. A, XPL (sample: 47); 4) sp. A, QPL (sample: 47); 5) sp. A SEM (sample: MAST); 6) Aggregate of sp. A, SEM (sample: 35); Figures 7 to 10 are of the same specimen. 7) sp. B, XPL (sample: 35); 8) sp. B, QPL (sample: 35); 9) sp. B, XPL (sample: 35); 10) sp. B, QPL (sample: 35); 11) sp. C, XPL (sample: 605); 12) sp. C, QPL (sample: 605); 13) sp. D, XPL (sample: 680); Figures 14 to 17 are of the same specimen. 14) sp. E, XPL (sample: L6); 15) sp. E, QPL (sample: L6). 16) sp. E, XPL (sample: L6); 17) sp. E, QPL (sample: L6). 18) sp. F, XPL (sample: 35); 19) sp. F, QPL (sample: 35); 20) sp. G, XPL (sample: L2).

established at the end of the Paleozoic: the partitioning of biolimiting metals allowed a major evolutionary innovation of coccolithophores in coastal settings as soon as ameliorated chemical conditions unlocked shallow-water niches to red algae.

Accelerated weathering of the Siberian Traps large igneous province and enhanced run-off intensified metal and nutrient recycling into the ocean as well as drew down atmospheric CO_2 (Jurikova et al. 2020) thus improving the carbonate saturation state of the ocean, possibly facilitating coccolithogenesis and/or nannofossil preservation. Weathering-induced CO_2 consumption was presumably a key factor in the relatively lower temperatures documented during the early Smithian (Romano et al. 2013). This phase was associated with an initial selective recovery of ammonoids, foraminifers and conodonts (Song et al. 2014) prior to a major warming event in the late Smithian (Romano et al. 2013; Galfetti et al. 2007; Zhao et al. 2020; Scotese et al. 2021), which was followed by another cooling episode in the latest Smithian (Zhao et al. 2020). Although framed by generally hot climatic conditions, cooler intervals may have increased temperature gradients, promoting more efficient oceanic circulation and facilitating the upwelling of nutrient-rich deep waters (Zhao et al. 2020).

Saito et al. (2022) investigated biomarkers (C33 *n*-alkyl cyclohexane) evidencing discrete spikes in the Lower Triassic Chaohu section (South China)

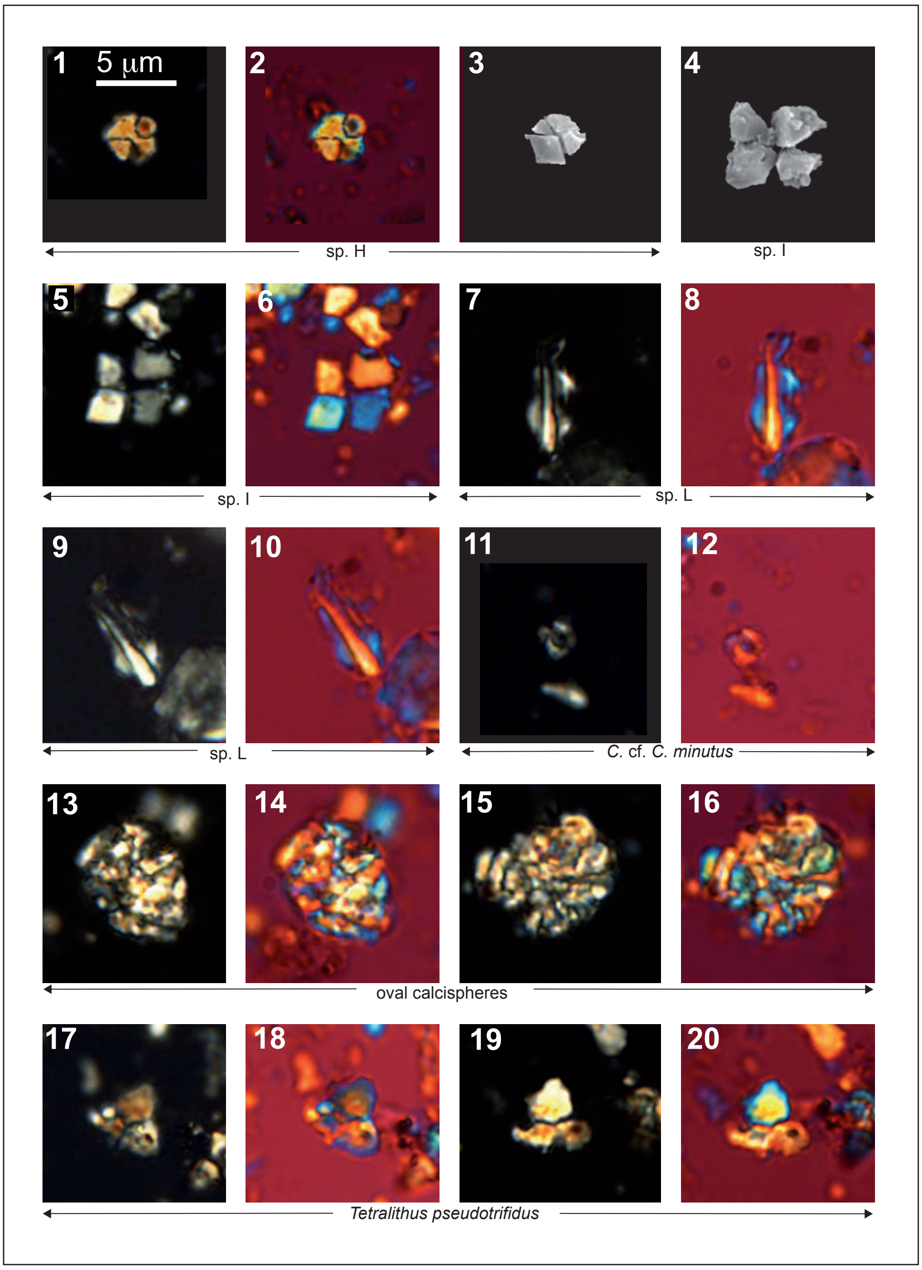

Plate 3

Calcareous nannofossils under light microscope in smear slides (XPL = cross-polarized light; QPL = cross-polarized light with quartz lamina), and under Scanning Electron Microscope (SEM). 1) sp. H, XPL (sample: C1); 2) sp. H, QPL (sample: C1); 3) sp. H, SEM (sample: 35); 4) sp. I, SEM (sample: 35); 5) sp. I, XPL (sample: 35); 6) sp. I, QPL (sample: 35); 7) sp. L, XPL (sample: 41); 8) sp. L, QPL (sample: 41); 9) sp. L, XPL (sample: 41); 10) sp. L, QPL (sample: 41); 11) *C.* cf. *C. minutus*, XPL (sample: 37); 12) *C.* cf. *C. minutus*, QPL (sample: 37); 13) oval calcisphere, XPL (sample: 224); 14) oval calcisphere, QPL (sample: 224); 15) oval calcisphere, XPL (sample: 37); 16) oval calcisphere, QPL (sample: 37); 17) *T. pseudotrifidus*, QPL (sample: 37). 18) *T. pseudotrifidus*, XPL (sample: 37); 19) *T. pseudotrifidus*, QPL (sample: 37); 20) *T. pseudotrifidus*, XPL (sample: 37).

that are interpreted as the results of phytoplankton blooms at the Permian/Triassic boundary, at the Induan/Olenekian boundary, in the Smithian and Spathian (Fig. 4). Most of these peaks are also documented in the Boreal area (Saito et al. 2022) and suggest supra-regional events induced by enhanced continental weathering and large fluxes into the ocean of terrestrial material, which fertilized marine phytoplankton triggering anoxia and delaying the benthic faunal recovery (Saito et al. 2022).

The Smithian nannofossils found in China correlate with an interval of enhanced phytoplankton blooms (Fig. 4). As observed after other mass extinctions and following speciation, heightened availability of nutrients and biolimiting metals may have started the evolution of coccolithophores and progressively increased diversity and abundance. The oldest and most persistent sp. A coccoliths found in South China morphometrically resemble simple liths produced by several extant coastal-neritic coccolithophores that often secrete small and poorly calcified coccoliths or are non-calcifying during the haploid stages (De Vargas et al. 2007). In the long evolutionary history of calcareous nannoplankton (Bown et al. 2004), major origination and/or rescue phases following environmental "extreme conditions" are characterized by the occurrence of tiny coccoliths. Moreover, small size is a common feature during the initial phase of the origination of several coccolithophore taxa in the Mesozoic (e.g. Mattioli & Erba 1999; Bornemann et al. 2003; Visentin et al. 2023).

After the exceptional acidification of surface waters in the Permian/Triassic boundary interval, an increase in alkalinity allowed the resumption of the neritic calcifying biota (Jurikova et al. 2020). The recovery during the Early to Middle Triassic was characterized by a stepwise renewal of benthic faunas (Payne et al. 2004; Chen & Benton 2012), including macroalgae, corals, and metazoan reefs (Fig. 4).The Lower Triassic nannofossils correlate with the appearance of many other new marine groups indicating that a major diversification was going on from the base to the top of the food chain. Moreover, our findings of Ladinian relatively diversified nannofossil assemblages (Fig. 3) correlate with new planktic organisms and the moving of fishes and reptiles from coastal to open sea environments (Kelley et al. 2014; Lu et al. 2018).

We question whether the origin of calcifying coccolithophores may have played a key role in driving the radiation, diversity, and abundance of marine vertebrates and fishes by contributing to a dietary shift from cyanobacteria and green algae to red algae. Globally, the early evolution of marine reptiles suggests that the transition from the 'Paleozoic Fauna' to the 'Modern Fauna' began in the Early Triassic (Rieppel 2000; McGowan & Motani 2003). The occurrence in South China of predatory marine tetrapods, fishes, bivalves, ammonoids and arthropods in the middle Spathian (Fu et al. 2016) indicates a fully habitable environment. The middle Spathian fish fauna reorganization supports the establishment of a new Mesozoic marine ecosystem some 3 myrs after the end-Permian extinction. During the late Spathian marine reptiles were quite diversified in coastal settings of the Panthalassa Ocean and their initial invasion into the ocean is dated as 248.81 Ma (Fu et al. 2016). This oceanic reorganization was interpreted as the result of the final breakdown of stratification and anoxia together with increased primary productivity (Fu et al. 2016).

The shift from a Paleozoic marine fauna to the Modern one (Martin & Quigg 2012) closely correlates with the beginning (Smithian) and early evolution (Spathian through Longobardian) of coccolithophore calcification.

The Lower Triassic nannofossils found in South China suggest a rapid adjustment of marine phytoplankton to a global paleoenvironmental crisis. However, there are no other data on Lower and Middle Triassic nannofossils to assess the abundance, diversity and distribution of calcareous nannoplankton beyond the area investigated here, thus it is not clear whether calcifying coccolithophores were widespread at this time or not. Based on the records of calcareous nannofossils in Norian-Rhaetian successions, Pérez Panera et al. (2023a) hypothesized that calcifying coccolithophores originated in the Western Tethys, from where they rapidly dispersed via oceanic currents to the Southeastern Tethys and subsequently across Panthalassa. Alternatively, their dispersal from the Western Tethys to the Eastern Pacific may have occurred intermittently through the Hispanic Corridor (Pérez Panera et al. 2023a). However, the Olenakian nannofossils from South China suggest that early coccolithophores were already present in Eastern Tethys (Fig. 1) indicating that they may have originated there and later expanded both westward and eastward via surface currents.

At the moment we can only speculate – but not exclude – that the modern ocean started with the Early Triassic (Smithian) inception of coccolithogenesis, although we are aware that only a wide distribution and high abundance of coccolithophores could have influenced biogeochemical cycles. In fact, the "Mid Mesozoic Revolution" (MMR) corresponds to substantial pelagic carbonate deposition caused by proliferation of calcareous plankton that drove a major change in the oceanic carbonate system dynamics (Ridgwell 2005). Smithian coccoliths from South China indicate phytoplankton calcification soon after extreme carbonate oversaturation ($\Omega > 9$) subsided in the earliest Triassic (Ridgwell 2005). Tectonic events like the breakup of Pangea and the opening of the Atlantic Ocean (Katz et al. 2007) occurred too late to explain this early onset of the MMR. Instead, the Siberian Traps' volcanism triggered accelerated weathering, reducing atmospheric CO_2 and improving seafloor oxygenation following widespread ecological collapse. These changes in ocean chemistry and redox state influenced nutrient and trace metal cycling. Under lower CO_2 and selective trace metal availability, some prymnesiophytes evolved calcification in the Early Triassic. This adaptation – driven by geological processes – transformed the oceanic ecosystem, biogeochemical cycles, and marine sedimentation. Our findings link the emergence of the modern ocean to the dawn of the Mesozoic.

Conclusions

The identification of calcareous nannofossils in the Lower and Middle Triassic succession in China provides important constraints on the origin and early history of coccolithophores. The most significant outcomes of our investigation are outlined below:

- the oldest coccoliths, dating back to the Smithian (Early Triassic, ~250 Ma), shift the origin of coccolithophore calcification approximately 40 million years earlier than previously established. This pushes the onset of coccolithogenesis into a critical window following the end-Permian mass extinction.
- Smithian coccoliths described here significantly narrow the temporal gap between molecular clock estimates for calcifying coccolithophore origins and their first fossil occurence.
- Olenekian primitive, simple and tiny coccoliths from South China suggest that early coccolithophore taxa emerged soon after a profound ecological disruptions.
- Early Triassic lowered CO_2 levels, coupled with increased nutrient availability, may have provided advantageous conditions for the calcification in haptophyte lineages.
- A marked increase in nannofossil diversity across the Smithian–Longobardian interval, particularly during the Ladinian, correlates with a major evolutionary pulse in fish lineages and a broader transition from Paleozoic to Modern marine faunas, highlighting the potential role of phytoplankton innovation in shaping post-extinction marine ecosystems.

In summary, our findings not only extend the fossil record of coccolithophores to the Early Triassic but also suggest interconnections between geological processes, ocean chemistry, and biological innovation. These insights mark an important step forward in reconstructing the early history of calcareous nannoplankton and the emergence of the modern ocean.

Taxonomic index of calcareous nannofossil taxa reported in this study

Archaeozygodiscus koessenensis Bown, 1985
Carnicalyxia Janofske, 1990
Crucirhabdus minutus Jafar, 1983
Crucirhabdus primulus Prins, 1969 ex Rood et al., 1973, emend Bown, 1987
Eoconusphaera hallstattensis Demangel et al., 2021
Prinsiosphaera triassica Jafar, 1983
Tetralithus pseudotrifidus Jafar, 1983

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