# Occurrence of Coccolithophorids in the Northeastern and Central South China Sea

Tien-Nan Yang<sup>(1)</sup>, Kuo-Yen Wei<sup>(1, 2)</sup> and Li-Ling Chen<sup>(1)</sup>

(Manuscript received 2 December, 2002; accepted 23 January, 2003)

**ABSTRACT:** Coccolithophorids in the northeastern and central South China Sea (SCS) were surveyed in March and October 1996. The cell density of coccolithophorids ranged from 25 x  $10^3$  cells L<sup>-1</sup> to 31 x  $10^3$  cells L<sup>-1</sup> in sea-surface water (0–25 m in depth), and from 12 x  $10^3$  cells L<sup>-1</sup> to 62 x  $10^3$  cells L<sup>-1</sup> in subsurface water (150 m in depth). The lowest cell number was recorded in the subsurface (150 m in depth) in the central gyral area, while the highest one was at the same depth in the northeastern realm. A total of thirty-one species were identified. The species richness in the northeastern SCS is higher than in the central area. *Emiliania huxleyi* (Lohmann) Hay et Mohler, *Gephyrocapsa oceanica* Kamptner, *Umbellosphaera* Paasche spp. and *Syracosphaera* Lohmann spp. dominated the surface assemblages, whereas *Florisphaera profunda* Okada et Honjo, *Gladiolithus flabellatus* (Halldal et Markali) Jordan et Chamberlain predominated in the subsurface layer. In contrast, *Palusphaera vandeli* Lecal emend. R. E. Norris presented in both surface and subsurface assemblages.

KEY WORDS: Biogeography, Cell number, Coccolithophorids, South China Sea.

# **INTRODUCTION**

Coccolithophorids are unicellular haptophytes commonly distributed throughout the photic and uppermost aphotic zones in the oceans, except in Polar areas (McIntyre et al., 1970), and are one of the world's major primary producers, contributing about 15 % of the average oceanic phytoplankton biomass in the ocean (Berger, 1976). Coccolithophorids produce minute (1-25  $\mu$ m), elaborate calcite plates (coccoliths) to form coccospheres, which are often incorporated into fecal pellets or marine snow and sink downward to the deep ocean (Honjo, 1976, 1978). In the modern ocean, the coccolithophorids may occupy at least 25%, and even up to 77% by weight, in the total recent marine sediments above the calcite compensation depth (Bramlette, 1958; Honjo, 1978; Deuser and Ross, 1989; Honjo, 1996), and thus represent a large proportion of the flux of particulates in the carbonate pump to the deep ocean. Furthermore, the widely distributed coccoliths and coccolithophorids in high concentration in the surface ocean during bloom seasons may form "white water" and enhances reflection of visible light back to the atmosphere (Ackleson et al., 1988; Brown, 1995; Balch et al., 1999), therefore, they have recently gained much attention as important players in global climate change and carbon and sulphur cycles (Westbroek *et al.*, 1993; Winter et al., 1994; Hagino et al., 2000; Cortés et al., 2001; Haidar and Thierstein, 2001; Burkill *et al.*, 2002).

The large-scale distribution of modern coccolithophorids in the open ocean has been studied in various parts of the world (Winter *et al.*, 1994 and references therein). About three decades ago, Okada and Honjo (1970; 1973) and Nishida (1979) conducted large-scale

<sup>1.</sup> Department of Geosciences, National Taiwan University, Taipei 106, Taiwan.

<sup>2.</sup> Corresponding author. E-mail: weiky@ms.cc.ntu.edu.tw Tel: +886-2-23691143. Fax: +886-2-23636095

coccolithophorid biogeographic studies in the Pacific Ocean with particular emphasis on the North Pacific. Okada and Honjo (1973) established six coccolithophorid zones in the surface waters along the 155°W meridian based on the distribution pattern of characteristic species. Recently, Hagino *et al.* (2000) documented the spatial dynamics of coccolithophorid assemblages in the western-central Equatorial Pacific Ocean, while Cortés *et al.* (2001) studied the temporal variation pattern of coccolithophorid in water column at the HOT station ALOHA, Hawaii. For the western boundary periphery of the Pacific, Okada and Honjo (1975) conducted a large-scale study of coccolithophorid biogeography of the western Pacific marginal seas. Yang *et al.* (2001) documented three coccolithophorid communities in surface waters off the northeastern Taiwan. For the South China Sea (SCS), the distribution pattern of calcareous nannofossils in surface sediments was documented by Chen and Shieh (1982) and Cheng (1992). However, for the living coccolithophorids only a limited study restricted in sea-surface of the southern part of SCS was done (Okada and Honjo, 1975).

The SCS is the largest marginal sea in the western tropical Pacific Ocean. It has wide continental shelves to the northwest and south and a deep basin reaching 4700 m deep in the center (Sverdrup *et al.*, 1942). The basin is connected to the open ocean through several passages between the surrounding landmasses and islands. Among the various passages, the Luzon Strait (sill depth ~1900 m) between Taiwan and Luzon Island is the only major channel allowing effective water exchange with the western North Pacific (Sverdrup *et al.*, 1942). In the strait, a branch of the Kuroshio flows into the SCS on the southern side, and a returning current feeds into the main path of Kuroshio on the northern side (Li *et al.*, 1998; Liang *et al.*, 2003).

The surface circulation in the SCS changes drastically with season in response to the alternating monsoons (Wyrtki, 1961). The weaker southwest (summer) monsoon winds drive an anticyclonic gyre mainly in the southern basin during June to September, while the stronger northeast (winter) monsoon winds force a cyclonic gyre covering the entire basin with an intensified southward jet along the coast of Vietnam from November to March (Wyrtki, 1961; Shaw and Chao, 1994; Liang *et al.*, 2000). Localized upwelling occurs in area off Vietnam during the summer monsoon season and off the Sunda Shelf and western Luzon during the winter monsoons (Chao *et al.*, 1996; Shaw *et al.*, 1996; Udarbe-Walker and Villanoy, 2001). The nutricline in the west of Luzon could be uplifted in winter by as much as 100 m (Gong *et al.*, 1992). The monsoon-forced upwelling brings the nutrient-laden water closer to the surface and supports phytoplankton bloom. The high chlorophyll concentration and primary production of the upwelling cells can be recognized from satellite imagery (Tang *et al.*, 1999; Liu *et al.*, 2002).

The present study focuses on the distribution and community structure of coccolithophorids in water columns, especially in the surface (0-25 m in depth) and subsurface (150 m) waters for a comparison between upper and lower layer of the euphotic zone in the northeastern (St 1, St 3 and St 7) and central SCS (St 23 and St 36) during March and October 1996 (Fig. 1).

# **MATERIALS AND METHODS**

#### **Sampling of coccolithophorids**

Seawater samples containing coccolithophorids were taken from two dozens of stations in the northeastern and central SCS during Cruise 186 of the R/V *Ocean Researcher III* from the 24<sup>th</sup> through the 28<sup>th</sup> March 1996 and Cruise 467 of the R/V *Ocean Researcher I* from the 23<sup>rd</sup>

October through 8<sup>th</sup> November 1996, respectively. A Seabird CTD-General Oceanic Rosette assembly with 12 Go-Flo bottles (volume of 10 l) was used to obtain seawater samples. To exclude the effects caused by diurnal vertical movement of water masses on distribution of coccolithophorids, we selected seven stations, where samples were collected at about noon. Those stations are: stations St 1, St 3 and St 7 from Cruise 186, and stations St 23, St 36, St 45 and St 52 from Cruise 467 (Fig. 1).

Seawater (either 1 or 2 l) obtained by the Go-Flo bottles was filtered on board through a Nuclepore<sup>®</sup> polycarbonate membrane (47 mm in diameter, pore size 0.4  $\mu$ m) by applying low-pressure (<100 mm Hg) generated by a vacuum pump. Each membrane with its filtered Petri-dishes containing membranes were put into a desiccator in the laboratory. A piece of



Fig. 1. Map, with isobaths (in meters), of the South China Sea. The solid dots with station numbers St 1, St 3 and St 7 of Cruise 186, and St 23, St 36, St 45 and St 52 of Cruise 467, respectively, indicate the studied sites in the northeastern and central SCS. Cruise was conducted in March and October 1996, respectively.

membrane, about 1 cm<sup>2</sup>, was cut and mounted onto an aluminum stub with double-sided tape, and was then coated with platinum using a HITACHI E101 ion sputter coater.

#### **Counting of coccospheres**

The coccospheres on the cut membrane portion were examined in horizontal rows and counted in a total of 320 randomly picked viewing fields under  $2000 \times$  magnification with a HITACHI S-2400 Scanning Electron Microscope (SEM). In addition, tens of extra fields were examined for rare species.

The number of coccospheres per liter of seawater was calculated as follows:

$$N_T = N_C \times \frac{925}{Sv}$$

where  $N_T$  is the number of total individuals of coccospheres per liter,  $N_C$  is the number of coccospheres counted in 320 viewing fields, Sv is the filtered volume of seawater, and the value 925 is a ratio constant of the area covered by particles on the membrane ( $9.62 \times 10^{-4} \text{ m}^2$ , diameter 35 mm) to that of the 320 fields examined (the length and width of each field under 2000 × magnification is about  $65\mu$ m and  $50\mu$ m, respectively). The ratio constant was derived as  $925 = 9.62 \times 10^{-4} \text{ m}^2 / 320 \times 3.25 \times 10^{-9} \text{ m}^2$ .

The counting of coccoliths from 320 viewing-fields is sufficient enough to capture the community structure of a sample based upon an empirical test coupled with rarefaction technique. A comparison between our results with that of Okada and Honjo (1975) and Winter *et al.* (1979), which counted 300 individuals, shows that our counting methods are better in fully reflecting the biodiversity.

#### Taxonomy

The identification of coccolithophorids is based mainly on the morphology of cells and coccoliths, and was conducted following the classification scheme outlined by Jordan and Kleijne (1994), except for *Michaelsarsia adriaticus* (Shiller) Manton *et al.*, *Gladiolithus flabellatus* (Halldal et Markali) Jordan et Chamberlain and *Syracosphaera dilatata* Jordan *et al.* adopted respectively from Manton *et al.* (1984), Jordan and Chamberlain (1993) and Jordan *et al.* (1993). Furthermore, some new associations of holococcolith-heterococcolith or holococcolith-holococcolith coccospheres documented recently by Cros *et al.* (2000) also were adopted in the present work. The species list of tallied coccolithophorid taxa in this study is shown in Table 1.

### RESULTS

#### **Cell number**

The cell number of coccolithophorids counted in 320 viewing-fields and calculated cell density in waters of the studied sites are presented in Table 2. The cell density in sea-surface water (0 – 25 m in depth) ranged from 25 x  $10^3$  cells L<sup>-1</sup> to 31 x  $10^3$  cells L<sup>-1</sup>, without showing much geographic disparity between the northeastern (St 1, St 3 and St 7) and central SCS (St 23 and St 36) during the studied periods. The largest number in subsurface water (150 m in depth) was documented in the St 1, with value of 62 x  $10^3$  cells L<sup>-1</sup>, while the lowest one was recorded in the St 36, with value of 12 x  $10^3$  cells L<sup>-1</sup>. As exceptions, two samples collected after the passing-by of a tropical storm at St 45 and St 52 in the eastern SCS contain abnormally low concentration of coccolithophorids with values of 6.5 x  $10^3$  cells L<sup>-1</sup> and 5.6 x  $10^3$  cells L<sup>-1</sup>, respectively.

March, 2003

Table 1. Species list of the coccolithophorid taxa recognized in the present study. The taxonomic scheme was based on Manton *et al.* (1984), Jordan and Chamberlain (1993), Jordan *et al.* (1993), Jordan and Kleijne (1994), and Cros *et al.* (2000).

Acanthoica quattrospina Lohmann Algirosphaera robusta (Lohmann) R. E. Norris (Plate II. 1) Alveosphaera bimurata (Okada et McIntyre) Jordan et Young (Plate I. 1) Corisphaera Kamptner sp. Coronosphaera mediterranea (Lohmann) Gaarder (Plate II. 2) Daktylethra pirus (Kamptner) R. E. Norris (Plate I. 2; 4) Discosphaera tubifera (Murray et Blackman) Ostenfeld (Plate II. 3) Emiliania huxleyi (Lohmann) Hay et Mohler (Plate II. 4) Florisphaera profunda Okada et Honjo var. profunda Okada et McIntyre (Plate II. 5) Gephyrocapsa ericsonii McIntyre et Bé (Plate II. 6) G. oceanica Kamptner (Plate III. 1) Gladiolithus flabellatus (Halldal et Markali) Jordan et Chamberlain (Plate III. 2) Helicosphaera carteri (Wallich) Kamptner var. carteri (Plate III. 3) Michaelsarsia adriaticus (Schiller) Manton et al. Ophiaster hydroideus (Lohmann) Lohmann emend. Manton et Oates (Plate III. 5; 6) O. reductus Manton et Oates Palusphaera vandeli Lecal emend. R. E. Norris (Plate IV. 1) Reticulofenestra punctata (Okada et McIntyre) Jordan et Young (Plate IV. 2) Rhabdosphaera clavigera Murray et Blackman Syracosphaera dilatata Jordan et al. S. exigua Okada et McIntyre (Plate IV. 4) S. nana (Kamptner) Okada et McIntyre S. nodosa Kamptner\* (Plate I. 5) S. orbiculus Okada et McIntyre S. ossa Loeblich Jr et Tappan (Plate V. 1) S. pirus Halldal et Markali (Plate V. 2; 4) S. pulchra Lohmann (Plate V. 3) S. rotula Okada et McIntyre Umbellosphaera irregularis Paasche U. tenuis (Kamptner) Paasche (Plate V. 5) Zygosphaera amoena Kamptner

\*An association species reported by Kamptner (1941) and Cros et al. (2000).

#### **Distribution of coccolithophorids**

A total of 31 coccolithophorid species were identified (Table 1). Some new associations of holococcolith-heterococcolith or holococcolith-holococcolith coccospheres documented by Cros *et al.* (2000) were also observed in the present study. In addition to those combinations documented by Cros *et al.* (2000), we found a new association of holococcolith -heterococcolith coccosphere *Helladosphaera cornifera* (Shiller) Kamptner, a holococco-lithophorid form of *Syracosphaera nodosa* Kamptner (Plate I. 3). SEM photographs of selected species, including major dominant forms, are shown in Plates I-V. Holococcolithophorid species are displayed in Plate I, while other heterococcolithophorid species are shown in Plates II-V.

*Emiliania huxleyi* (Lohmann) Hay et Mohler, *Gephyrocapsa oceanica* Kamptner, *Umbellosphaera* Paasche spp. and *Syracosphaera* Lohmann spp. dominated in the surface water (Fig. 2), and *Florisphaera profunda* Okada et Honjo *Gladiolithus flabellatus* (Halldal et Markali) Jordan et Chamberlain predominated in subsurface layer (Fig. 3), whereas

Table 2. List of sampling time and number of coccolithophorid cells counted in 320 viewing-fields of each taxon recognized in samples recovered from different water levels at Stations St 1, St 3 and St 7, and St 23, St 36, St 45 and St 52, during ORIII Cruise 186 and ORI Cruise 467, respectively. The densities of coccolithophorid cells per liter were shown in the last row. The complete names of genera are referable ed in Table 1.

Cruise		ORIII C186						ORI C467				
Station	1		3	7		23	36		45	52		
Sampling time		Mar. 24		Mar. 25	Mar. 26		Oct. 28	Nov. 1		Nov. 3	Nov. 4	
Sample depth (m)	0	25	150	0	0	150	0	0	150	3	3	
A. quattrospina	0	0	0	0	0	0	1	0	0	0	0	
A. robusta	0	0	2	0	0	0	0	0	1	0	0	
A. bimurata	0	0	0	0	0	1	0	0	0	0	0	
Corisphaera sp.	1	0	0	0	0	0	0	0	0	0	0	
C. mediterranea	0	1	0	0	0	0	0	0	0	0	0	
D. pirus	0	0	0	0	0	2	0	0	0	0	0	
D. tubifera	1	0	0	0	2	0	1	0	0	0	0	
E. huxleyi	4	1	12	4	5	1	0	2	2	0	0	
F. profunda	0	0	9	0	0	4	0	0	5	0	0	
G. ericsonii	0	1	0	1	2	0	0	0	0	0	0	
G. oceanica	0	0	2	2	2	0	5	6	5	2	3	
G. flabellatus	0	0	2	0	0	4	0	0	0	0	0	
H. carteri	1	0	0	0	0	0	0	1	0	0	0	
M. adriaticus	0	0	1	0	0	0	1	0	0	0	0	
O. hydroideus	0	0	1	0	0	0	1	3	0	0	0	
O. reductus	0	0	2	0	0	0	0	1	0	0	0	
P. vandelii	12	14	35	12	9	15	12	3	0	0	0	
R. punctata	1	3	0	1	2	0	0	0	0	0	0	
R. clavigera	2	0	0	2	1	0	0	0	0	0	0	
S. dilatata	1	0	0	0	0	0	2	2	0	0	0	
S. exigua	0	0	0	0	0	0	3	0	0	0	0	
S. nana	1	0	0	0	0	0	0	0	0	0	0	
S. nodosa	1	1	0	0	0	0	0	0	0	0	0	
S. orbiculus	0	0	0	0	0	0	0	1	0	0	0	
S. ossa	2	0	0	0	1	0	0	0	0	0	0	
S. pirus	1	1	0	0	1	0	1	0	0	0	0	
S. pulchra	0	1	0	1	1	0	0	0	0	0	0	
S. rotula	0	0	0	0	0	1	0	0	0	0	0	
S. spp.	2	2	0	1	2	0	0	0	0	0	0	
U. irregularis	0	0	0	1	3	0	9	9	0	5	0	
U. tenuis	0	0	1	2	3	0	4	5	0	0	0	
Z. amoena	1	0	0	0	0	0	0	0	0	0	0	
Miscellaneous	0	0	0	0	0	0	1	0	0	0	3	
Cell counted	31	25	67	27	34	28	41	33	13	7	6	
Density (x1000 L <sup>-1</sup> )	29	23	62	25	31	26	25	31	12	6.5	5.6	

*Palusphaera vandeli* Lecal emend. R. E. Norris presented in both surface and subsurface assemblages. *E. huxleyi* is widely distributed in the area with a declining trend from the northeastern to central region. The relative abundance of *P. vandeli* shows a similar trend as *E. huxleyi*. In contrast, the relative abundances of *G. oceanica* and *Umbellosphaera* spp. exhibit an increasing trend from the northeastern to the central area. Meanwhile, the relative abundances of *Syracosphaera* spp., *F. profunda* and *G. flabellatus* do not vary much in the studied area. Generally speaking, surface communities (Fig. 2) are more diverse than the subsurface ones (Fig. 3), while the latter are characterized by the deep dwellers including *Algirosphaera robusta*, *Florisphaera profunda*, and *Gladiolithus flabellatus*.





Plate I. Five species of holococcolithophorids. 1: *Alveosphaera bimurata* (Okada et McIntyre) Jordan et Young. Collapsed monomorphic coccosphere consisting of lozenge-shaped caneoliths (St 7, 150 m); 2 & 4: *Daktylethra pirus* (Kamptner) R. E. Norris. 2: Disintegrated monomorphic coccosphere consisting of aeroliths (St 7, 0 m); 4: Magnified view of Figure 2, showing detail structure of aeroliths; 3: *Syracosphaera nodosa* Kamptner. *Helladosphaera cornifera*, holococcolithophorid form of *Syracosphaera nodosa*. Dimorphic coccosphere consisting of helladoform circum-flagellar coccoliths (arrows) and zygoform body coccoliths (St 1, 0 m); 5: *Poritectolithus maximus* Kleije. Dimorphic coccosphere with helladoform circum-flagellar coccoliths (arrows) and zygolith-like body coccoliths (St 36, 0 m); 6: *Syracolithus quadriperforatus* (Kamptner) Garder in Haimdal et Gaarder. Disintegrated monomorphic coccosphere consisting of laminoliths (St 7, 0 m). Figs. 1, 3, 4 & 6: bar = 1  $\mu$ m; fig. 2: bar = 5  $\mu$ m; fig. 5: bar = 2  $\mu$ m.



Plate II. Exhibited are all heterococcolithophorid species. 1: Algirosphaera robusta (Lohmann) Norris. Dimorphic coccosphere consisting of body and circum-flagellar sacuuliform rhabdoliths (arrows) (St 1, 150 m); 2: Coronosphaera mediterranea (Lohmann) Gaarder in Gaarder et Heimdal. Collapsed dimorphic coccosphere consisting of circum-flagellar caneoliths with a thick spine (arrows) and body caneoliths (St 1, 25 m); 3: Discosphaera tubifera (Murray et Blackman) Ostenfeld. Monomorphic coccosphere bearing salpingiform rhabdoliths (St 1, 0 m); 4: Emiliania huxleyi (Lohmann) Hay et Mohler. Coccosphere with distal shield elements and some detached placoliths (St 1, 0 m); 5: Florisphaera profunda Okada et Honjo var. profunda Okada et McIntyre. Coccosphere consisting of coccoliths with proximal view of the quadrangular plates (St 1, 150 m); 6: Gephyrocapsa ericsonii McIntyre et Bé. Coccosphere consisting of oval to elliptical placoliths, bearing highly arched bridge (St 1, 0 m). Figs. 1 & 4-6: bar = 1  $\mu$ m; figs. 2 & 3: bar = 2  $\mu$ m.



Plate III. Exhibited are all heterococcolithophorid species. 1: *Gephyrocapsa oceanica* Kamptner. Coccosphere consisting of oval placoliths. A bridge of two elements arches obliquely across the central pore on the distal shield (St 1, 150 m); 2: *Gladiolithus flabellatus* (Halldal et Markali) Jordan et Chamberlain. Dimorphic coccosphere bearing tubular coccoliths and lepidoliths. Tubular coccoliths hollow, with six-sides, tightly arranged around the cell. Lepidoliths flat, oval, proximally unmarked, distally with a groove along the short axis, arranged at the base of the tubular coccoliths (St 1, 150 m); 3: *Helicosphaera carteri* (Wallich) Kamptner var. *carteri*. Coccosphere bearing helicoliths (St. 1, 0 m); 4: *Michaelsarsia elegans* Gran emend. Manton *et al.* Polymorphic coccosphere bearing body caneoliths associated with link coccoliths (A) and ring coccoliths (B) (St. 1, 150 m); 5 & 6: *Ophiaster hydroideus* (Lohmann) Lohmann emend. Manton et Oates. 5: Polymorphic coccosphere bearing body caneoliths and circum-flagellar caneoliths (arrow) associated with link coccoliths (A) (St. 1, 150 m); 6: Magnified view of Figure 5. Showing detailed structure of body caneoliths and circum-flagellar caneoliths (arrow). Figs. 1 & 6: bar = 1  $\mu$ m; figs. 2-4: bar = 2  $\mu$ m; fig. 5: bar = 5  $\mu$ m.



Plate IV. Exhibited are all heterococcolithophorid species. 1: *Palusphaera vandeli* Lecal emend. R. E. Norris. Detached styliform rhabdoliths (St 1, 0 m); 2: *Reticulofenestra punctata* (Okada et McIntyre) Jordan et Young. Very small coccosphere consisting of small placoliths with central area partly covered by a basal plate and grills (St 1, 25 m); 3: *Syracosphaera molischii* Shiller. Disintegrated dithecate coccosphere (exotheca not shown), dimorphic endotheca consisting of body caneoliths (circum-flagellar caneolith not shown) (St 1, 0 m); 4: *S. exigua* Okada et McIntyre. Collapsed dithecate coccosphere with monomorphic endotheca; caneoliths have a horizontal, ridged distal flange and a central area with an elongate narrow central mound; cyrtoliths (arrows) elliptical, convex, with an irregular pattern of overlapping elements on the distal side (St 23, 0 m); 5: *S. halldalii* Jordan et Green. Coccosphere dimorphic consisting of body caneoliths and circum-flagellar caneoliths (arrows) (St 1, 150 m); 6: *S. lamina* Lecal-Schlauder. Coccosphere bearing caneoliths (St 36, 150 m). Figures exhibited are all heterococco- lithophorid species. Figs. 1-5: bar = 1  $\mu$ m; fig. 6: bar = 5  $\mu$ m.



Plate V. Five species of heterococcolithophorids. 1: *Syracosphaera ossa* Loeblich Jr et Tappan. Collapsed dimorphic coccosphere consisting of one circum-flagellar caneolith (arrow) and body caneoliths (St 1, 0 m); 2, 4: *S. pirus* Halldal et Markali. 2: Dithecate (exotheca not shown), endotheca dimorphic coccosphere consisting of caneoliths with a thick nodular protrusion in the central area (St 1, 0 m); 4: Magnified view of Figure 2, showing detailed structure of caneoliths; 3: *S. pulchra* Lohmann. Disintegrated dithecate, endotheca dimorphic coccosphere; cyrtolith (A) with depression in the central area; circum-flagellar caneoliths (arrow) and body caneoliths (St 1, 25 m); 5: *Umbellosphaera tenuis* (Kamptner) Paasche. Coccosphere with variation and overlap in size of umbelloliths (St 1, 25 m); 6: *Umbilicosphaera hulburtiana* Gaarder. Coccosphere with placoliths, central area surrounded by a row of nodules (arrow) on elements of the distally widening central tube (St 1, 25 m). Figs. 1, 3 & 6: bar = 1  $\mu$ m; fig. 2: bar = 10  $\mu$ m; fig. 4: bar = 5  $\mu$ m; fig. 5: bar = 2  $\mu$ m.



Fig. 2. Relative abundance of predominant coccolithophorids in surface water (0-3 m in depth) of the studied sites in the northeastern and central SCS.

#### DISCUSSION

Our current study (focusing on northern and central SCS) together with the previous study of the southern South China Sea of Okada and Honjo (1975) allows us to have a better sketch of the geographic distribution of modern coccolithophorids in the basin.

In general, the coccolithophorids recognized in the studied areas are similar to Okada and Honjo (1975) despite that we observed more species (24) than they did (20). Mirrored to the sedimentary pattern documented by Cheng (1992), *E. huxleyi* dominated in the northeastern area and its relative abundance declines meridionally to the south. Reciprocally, *G. oceanica* is more abundant than *E. huxleyi* in the central and southern realm. *P. vandeli*, an oceanic species characteristic of Kuroshio (Yang *et al.*, 2001), dominated in the northeastern and



Fig. 3. Relative abundance of dominant coccolithophorids in subsurface water 150 m depth at three studied sites in the northeastern and central SCS.

central SCS, but not reported by Okada and Honjo (1975) in the southern SCS. The intrusion of Kuroshio and entrapment of Pacific open-ocean waters in the northern and central SCS (Liang *et al.*, 2003) might have caused the occurrence of this species in the studied area and less so to the southern part. To a great extent, the distribution pattern of dominant taxa in the northern and central areas is consistent with that of calcareous nannofossils in surface sediments of seafloor (Cheng, 1992), although most of the holococcolithophorids not found in sedimentary assemblages due to their high susceptibility to dissolution.

The effect of tropical storm on coccolithophoirds is incidentally documented for the first time in the current study. Prior to our visit of St 45 and St 52, a tropical storm 35W was formed over the Philippines and moved westward and dissipated over Southeast Asia from October 31 through November 4, 1996. From satellite imagery retrieved from the Joint Typhoon Warning Center (http://metoc.npmoc.navy.mil/jtwc/atcr/1996atcr/pdf/wnp/35w.pdf),

the cloud covered almost three quarters of the SCS and it thus might produce heavy rainfall and cause strong dilution of the surface waters of central SCS. The coccolithophorids at St 45 and St 52 were collected on Nov. 3 and 4, three days after the passing-by of the storm. Only a few coccospheres of *G.oceanica* and *Umbellosphaera irrigularis* and several miscellaneous species were found. The cell densities were the lowest amongst all the counted samples. Other common species normally observed in the central SCS such as *P. vandeli* and *Syracosphaera* spp. were completely missing. Because the surviving species, *Umbellosphaera irrigularis*, is a species adapted to extremely low nutrient condition (Young, 1994; Yang *et al.*, 2001), it implies that the generally acknowledged typhoon-induced enhancement of phytoplankton productivity did not occur. As pointed out recently by Lin (personal communication), whether the storm mixed the surface waters down to the depth of nutricline and brought nutrients up to the surface is a determining factor for phytoplankton bloom. It appears that the tropical storm W35 was catastrophic to the surface-water community of coccolithophorids without inducing an intermediate enhancement of nutrient availability.

# ACKNOWLEDGEMENTS

The authors would like to thank Meng-Yang Lee, officers and crew of *R/Vs Ocean Researcher I* and *III* for helping collecting samples and hydrographic data. We are grateful to two anonymous reviewers for their constructive comments and corrections. This study was funded by grants of NSC-86-2611-M-002-005-K2 and NSC-86-2815-C-002-033-M from the National Science Council of the Republic of China.

#### LITERATURE CITED

- Ackleson, S., W. M. Balch and P.M. Holligan. 1988. White waters of the Gulf of Maine. Oceanogr. 1: 18-22.
- Balch, W. M., D. T. Drapeau, T. L. Cucci, R. D. Vaillancourt, K. A. Kilpatrick and J. J. Fritz. 1999. Optical backscattering by calcifying algae, separating the concentration of particulate inorganic and organic carbon fractions. J. Geophys. Res. 104: 1541-1558.
- Berger, W. H. 1976. Biogenous deep-sea sediments: production, preservation and interpretation. In: Riley, J. P. and R. Chester (eds.). Chemical Oceanography 5: 265-383.
- Bramlette, M. N. 1958. Significance of coccolithophorids in calcium-carbonate deposition. Geol. Soc. Amer. Bull. 69: 121-126.
- Brown, C. W. 1995. Global distribution of coccolithophore blooms. Oceanogr. 8: 59-60.
- Burkill, P. H., S. D. Archer, C. Robinson, P. D. Nightingale, S. B. Groom, G. A. Tarran and M. V. Zubkov. 2002. Dimethylsuphide biogeochemistry within a coccolithophore bloom (DISCO): an overview. Deep-Sea Res. II, 49: 2863-2885.
- Chao, S.-Y., P.-T. Shaw and S.-Y. Wu. 1996. Deep water ventilation in the South China Sea. Deep-Sea Res. I, **43**: 445-466.
- Chen, M.-P. and K.-S. Shieh. 1982. Recent nannofossil assemblages in sediments from Sunda Shelf to Abyssal Plain, South China Sea. Proc. Nat. Sci. Council (Taiwan, ROC), Part A, 6: 250-285.

- Cheng, X. 1992. Calcareous nannofossils in surface sediments of the central and northern parts of the South China Sea. J. Micropal. **11**: 167-176.
- Cortés, M. Y., J. Bollmann and H. R. Thierstein. 2001. Coccolithophore ecology at the HOT station ALOHA, Hawaii. Deep-Sea Res. II, **48**: 1957-1981.
- Cros, L., A. Kleijne, A. Zeltner, C. Billard and J. R. Young. 2000. New examples of holococcolith-heterococcolith combination coccospheres and their implications for coccolithophorid biology. Mar. Micropal. **39**: 1-34.
- Deuser, W. G. and E. H. Ross. 1989. Seasonally abundant planktonic foraminifera of the Sargosso Sea, deep-water fluxes, isotopic compositions, and paleoceanographic implications. J. Foram. Res. **19**: 268-293.
- Gong, G.-C., K.-K. Liu, C.-T. Liu and S.-C. Pai. 1992. The chemical hydrography of the South China Sea west of Luzon and a comparison with the West Philippine Sea. TAO **3**: 587-602.
- Hagino, K., H. Okada and H. Matsuoka. 2000. Spatial dynamics of coccolithophore assemblages in the equatorial western-central Pacific Ocean. Mar. Micropaleont. **39**: 53-72.
- Haidar, A. T. and H. R. Thierstein. 2001. Coccolithophore dynamics off Bermuda (N. Atlantic). Deep-Sea Res. II, **48**: 1925-1956.
- Honjo, S. 1976. Coccoliths: Production, transportation and sedimentation. Mar. Micropaleont. 1: 65-79.
- Honjo, S. 1978. Sedimentation of materials in Sargasso Sea at a 5367 m station. J. Mar. Res. 36: 469-492.
- Honjo, S. 1996. Fluxes of particles to the interior of the open oceans. In: Ittekkot, V. *et al.* (eds.). Particles Flux in the Ocean. Scope **57**: 91-154. Wiley, N. Y.
- Jordan, R. W. and A. H. L. Chamberlain. 1993. Vexillarius cancellifer gen. sp. nov., and its possible affinities with other living coccolithophorids. In: Hamrsmíd, B. and J. R. Young (eds.). Nannoplankton Research Vol. 2. Tertiary biostratigraphy and paleoecology; Quaternary coccoliths. pp. 305-325. [Knihovnicka zemnio plynu a nafty, 14b.]
- Jordan, R. W, A. Kleijne and B. R. Heimdal 1993. Proposed changes to classification system of living coccoithophorids. III. INA Newsl. **15**: 18-22.
- Jordan, R. W and A. Kleijne. 1994. A classification system for living coccolithophores. In: Winter, A. and W. G. Siesser (eds.). Coccolithophores. pp. 83-105. Cambridge University press. U. K.
- Kamptner, E. 1941. Die Coccolithineen der Südwestküste von Istrien. Naturh. Mus. Wien, Ann. Anz. **51**: 54-149.
- Li, L., W. D. Nowlin and S. Jilan. 1998. Anticyclonic rings from the Kuroshio in the South China Sea. Deep-Sea Res. I, **45**: 1469-1482.
- Liang, W.-D., J.-C. Jan and T.-Y. Tang. 2000. Climatological wind and upper ocean heat content in the South China Sea. ACTA Oceangr. Taiwanica **38**: 91-114.
- Liang, W.-D., T.-Y. Tang, Y.-J. Yang, M.-T. Ko and W.-S. Chuang. 2003. Upper ocean current around Taiwan. Deep-Sea Res. II. (In press)
- Liu, K.-K., S.-Y. Chao, P.-T. Shaw, G.-C. Gong, C.-C. Chen and T.-Y. Tang. 2002. Monsoon-forced chlorophyll distribution and primary production in the South China Sea: Observations and a numerical study. Deep-Sea Res. I, **49**: 1387-1412.
- Manton, I., G. Bremer, and K. Oates. 1984. Nanoplankton from the Galapagos Islands. *Michaelsarsia elegans* Gran and *Halopappus adriaticus* Schiller (coccolithophorids) with special reference to coccoliths and their unmineralized components. Philosophical

Transactions of the Royal Society of London B 305: 183-199.

- McIntyre, A., A. W. H. Bé and M. B. Roche. 1970. Modern Pacific coccolithophorida: a paleontological thermometer. Trans. N. Y. Acad. Sci. **32**: 720-31.
- Nishida, S. 1979. Atlas of Pacific Nannoplanktons. News of Osaka Micropaleontologists, Special Paper, No. 3, 31 pp., 23 pls.
- Okada, H. and S. Honjo. 1970. Coccolithophoridae distribution in Southwest Pacific. Pacif. Geol. 2: 11-21.
- Okada, H. and S. Honjo. 1973. The distribution of oceanic coccolithophorids in the Pacific. Deep-Sea Res. **20**: 355-374.
- Okada, H. and S. Honjo. 1975. Distribution of coccolithophores in marginal seas along the Western Pacific Ocean and in the Red Sea. Mar. Biol. **31**: 271-285.
- Shaw, P.-T. and S.-Y. Chao. 1994. Surface circulation in the South China Sea. Deep-Sea Res. I, **41**: 1663-1683.
- Shaw, P.-T., S.-Y. Chao, K.-K. Liu, S.-C. Pai and C.-T. Liu. 1996. Winter upwelling off Luzon in the north-eastern South China Sea. J. Geophy. Res. 101: 16435-16448.
- Sverdrup, H. U., M. W. Johnson and R. H. Fleming. 1942. The Oceans. Prentice Hall, New York. 1087pp.
- Tang, D.-L., I.-H. Ni, D. R. Kester and F. E. Müller-Karger. 1999. Remote sensing observations of winter phytoplankton blooms southwest of the Luzon Strait in the South China Sea. Mar. Ecol. Prog. Ser. 191: 43-51.
- Udarbe-Walker, M. J. B. and C. L. Villanoy. 2001. Structure of potential upwelling areas in the Philippines. Deep-Sea Res. I, **48**: 1499-1518.
- Westbroek, P., C. W. Brown, J. van Bleijswijk, C. Brownlee, G. J. Brummer, M. Conte, J. Egge, E. Fernández, R. W. Jordan, M. Knappertsbusch, J. Stefels, M. Veldhuis, P. van der Wal and J. R. Young. 1993. A model system approach to biological climate forcing. The example of *Emiliania huxleyi*. Glo. Plan. Change 8: 27-46.
- Winter, A., Z. Reiss and B. Luz. 1979. Distribution of living coccolithophore assemblages in the Gulf of Elat ('Aqaba). Mar. Micropaleontol. 4: 197-223.
- Winter, A., R. W. Jordan and P. H. Roth. 1994. Biogeography of living coccolithophores in ocean waters. In: Winter, A. and W. G. Siesser (eds.). Coccolithophores. pp. 161-177. Cambridge University Press, U. K.
- Wyrtki, K. 1961. Physical oceanography of the south-east Asian waters. NAGA Report Vol. 2, Scientific Results of Marine Investigations of the South China Sea and the Gulf of Thailand. Scripps Institution of Oceanography, La Jolla, CA, 195pp.
- Yang, T.-N., K.-Y. Wei and G.-C. Gong. 2001. Distribution of coccolithophorids and coccoliths in surface ocean off northeastern Taiwan. Bot. Bull. Acad. Sinica 42: 287-302.

# 南中國海東北部及中部之鈣板藻 楊天南<sup>(1)</sup>、魏國彥<sup>(1,2)</sup>、陳俐陵<sup>(1)</sup> (收稿日期:2002年12月2日;接受日期:2003年1月23日)

# 摘 要

本研究檢視 1996 年 3 月及 10 月分別在南中國海東北部及中部採得之海水樣本中所 含之鈣板藻族群。鈣板藻密度在 0-25 公尺的海表水為每公升 25 x 10<sup>3</sup> 至 31 x 10<sup>3</sup> 細 胞,而在次表水 150 公尺深處則為每公升 12 x 10<sup>3</sup> 至 62 x 10<sup>3</sup> 細胞。在南海中部 150 公尺水深之次表水層的鈣板藻量最低,而在東北部之次表層水則紀錄到最高量。所鑑定 出鈣板藻共屬 31 種,種歧異度以東北部的表水層較高。海表層的優勢種屬為 Emiliania huxleyi (Lohmann) Hay et Mohler, Gephyrocapsa oceanica Kamptner, Umbellosphaera Paasche spp.和 Syracosphaera Lohmann spp.,至於次表水層則以 Florisphaera profunda Okada et Honjo和 Gladiolithus flabellatus (Halldal et Markali) Jordan et Chamberlain 為優勢 種,而 Palusphaera vandeli Lecal emend. R. E. Norris 則在表水層和次表水層皆佔有相當 高的比例。

關鍵詞:生物地理、細胞數、鈣板藻、南中國海。

 <sup>1.</sup> 國立台灣大學地質科學系,台北市 106 羅斯福路4段1號,台灣。
2. 通信作者。