J. Nannoplankton Res. **29** (2), 2007, pp.78-87
ISSN 1210-8049 Printed by Cambridge University Press, UK

Living *Braarudosphaera bigelowii* (Gran & Braarud) Deflandre in the Bering Sea

Susumu Konno
Division of Interactive Symbiosphere Sciences, Graduate School of Science & Engineering, Yamagata University, 1-4-12 Kojirakawa-machi, Yamagata 990-8560, Japan
Naomi Harada
Institute of Observational Research for Global Change, Japan Agency for Marine-Earth Science & Technology, 2-15 Natsushima-cho, Yokosuka 237-0061, Japan
Hisashi Narita
Department of Marine Science, School of Marine Science & Technology, Tokai University, 3-20-1 Orido, Shimizu-ku, Shizuoka 424-8610, Japan
Richard W. Jordan*
Department of Earth & Environmental Sciences, Faculty of Science, Yamagata University, 1-4-12 Kojirakawa-machi, Yamagata 990-8560, Japan; *sh081@kdw.kj.yamagata-u.ac.jp

Manuscript received 2nd May, 2007; revised manuscript accepted 15th September, 2007

Abstract During the MR06-04 cruise of the *R/V Mirai* in summer, 2006, surface and subsurface water-samples were extensively collected from the eastern Bering Sea. In a small number of these samples, *Braarudosphaera bigelowii* was detected in relatively low absolute abundances. Their presence in the Bering Sea may represent the highest boreal-latitude occurrence reported so far. Scanning electron microscope observations have revealed the presence of two types of coccosphere, one with flattened faces, and one with somewhat concave faces. Regardless of this coccosphere morphology, most of the pentalith dimensions correspond to the so-called 'intermediate B' form. The coccospheres of *B. bigelowii* were mostly found in an area associated with a mesoscale bloom of *Emiliania huxleyi*. The hydrographic conditions of this bloom water generally support the hypothesis that *B. bigelowii* prefers low-salinity, nutrient-rich coastal waters. Here, we report on the ecology and distribution of *B. bigelowii*, as well as the morphology of the two coccosphere types and their taxonomic significance.

Keywords Bering Sea, *Braarudosphaera bigelowii*, living nannoplankton assemblages, morphology

1. Introduction

Although there are numerous and well documented reports of coccolithophorids from the North Pacific (*e.g.* Okada & Honjo, 1973; Nishida, 1979; Reid, 1980; Hagino, 1997; Hagino *et al*., 2000), few studies have dealt with their presence in the Bering Sea. In fact, most of the Bering Sea papers relate to the recent occurrence of *Emiliania huxleyi* blooms on the eastern continental shelf (Sukhanova & Flint, 1998; Vance *et al*., 1998; Stockwell *et al*., 2001; Olson & Strom, 2002; Shin *et al*., 2002; Merico *et al*., 2004; Nishitani & Zhang, 2005). Of those that have recorded the coccolithophorid assemblages in other parts of the Bering Sea, the general picture seems to be one of low diversity and low abundance, with *E. huxleyi* and *Coccolithus pelagicus* being the main two components (Takahashi *et al*., 2002; Tanimoto *et al*., 2003; Hattori *et al*., 2004).

Micranthrolithus was the most abundant braarudospherid throughout much of the Early Cretaceous, before *Braarudosphaera* replaced it in the mid-Cretaceous, with *Braarudosphaera*-rich sediments being laid down during the Turonian in various locations around the world (Cunha & Shimabukuro, 1997; Burnett *et al*., 1998; Svábenická, 1999). *Braarudosphaera* became less abundant during the Late Cretaceous and Paleocene, but there were consistent occurrences in the Eocene, as well as exceptional intervals like the Cretaceous/Tertiary boundary (Bown, 2005). *Braarudosphaera* declined again after the Eocene, and this general trend continued throughout the Late Cenozoic, apart from sporadic occurrences of *Braarudosphaera*-rich sediments during the Oligocene (Parker *et al*., 1985; Siesser *et al*., 1992; Peleo-Alampay *et al*., 1999; Kelly *et al*., 2003).

In the last 50 years, many coccolith workers have reported the presence of *Braarudosphaera* in the surface-sediments of nearshore environments, especially around Japan (Takayama, 1972; Nishida & Konda, 1974; Nishida, 1981; Tanaka, 1991), but also in other parts of the world (Martini, 1967; Scholle & Kling, 1972; Bukry, 1974; Zhang & Siesser, 1986; Ferreira & Cachão, 2005; Giunta *et al*., 2007). Today, *Braarudosphaera* can be found in the Norwegian Sea (Heimdal, 1993), in coastal waters off Portugal (Duarte-Silva *et al*., 2004), off western North Africa (Lecal-Schlauder, 1950, as '*B. Deflandrei*'; Heimdal & Gaarder, 1981), in the Mediterranean Sea (Borsetti & Cati, 1972; Knappertsbusch, 1993), off eastern North America (Gran & Braarud, 1935; Bérard-Therriault *et al*., 1999), in the Sargasso Sea (Gaarder, 1954; Hulburt, 1962; Hulburt & Rodman, 1963), in the Gulf of Panama (Smayda, 1966), off Australia (Hiramatsu & De Deckker, 1996; Takahashi & Okada, 2000), off Japan (Hagino, 1997; Takano *et al*., 2006), and in the North Pacific (Nishida, 1979). It should be noted that *Braarudosphaera bigelowii* has also been

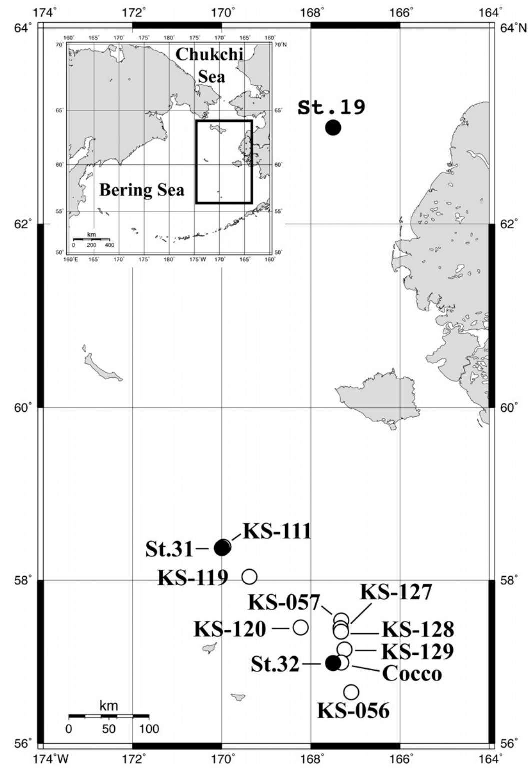


Figure 1: General location of the study area (inset) and location of the samples containing *B. bigelowii*. Black circles indicate CTD stations, open circles indicate underway sites. Maps created using Martin Weinelt's 'Online Map Creation' site at www.aquarius.ifm-geomar.de

recorded in sediment trap studies from the Bay of Biscay (Beaufort & Heussner, 2001) and the Sea of Okhotsk (Broerse *et al.*, 2000), although living populations have not been reported from either of these two locations. In general, the absolute abundance of *B. bigelowii* is low and it is usually a rare component in nannoplankton assemblages, however, Duarte-Silva *et al.* (2004) reported cell concentrations of up to 110 x 10^3 cells/litre.

Here, we report the finding of *Braarudosphaera* coccospheres in Bering Sea surface-waters, possibly for the first time, and perhaps from the highest latitude.

2. Material and methods

During Leg 2 of the MR06-04 cruise of the *R/V Mirai* (a research ship belonging to the Japan Agency for Marine-Earth Science & Technology - JAMSTEC), in the summer of 2006, surface and subsurface water-samples were collected at various stations in the Bering Sea. Most surface-water samples were acquired while the ship was underway, using the shipboard sea-water supply (for research use), which is obtained *via* an intake pipe located 4m below the ship. In the case of these underway samples, 1-4l of sea-water were collected in plastic bottles with the following information recorded at the time of sampling: the date and (Greenwich Mean) time, geographic coordinates, and those parameters (such as temperature, salinity, fluorescence and dissolved oxygen) being continuously recorded by instruments connected to the sea-water supply. Of the 165 samples collected using this method during Leg 2 of MR06-04, only eight are presently known to contain *Braarudosphaera* coccospheres (see Figure 1, Table 1). These samples were given a 'KS' notation (the initials of the sample collector, Konno Susumu) to distinguish them from Conductivity Temperature Depth (CTD) sites (labeled 'St.'). An additional underway sample, labeled 'Cocco', was obtained by Hisashi Narita.

Subsurface samples were obtained using a rosette of water-bottles attached to a CTD rig, with about three to eight depths selected from each of the 15 shallow and deep hydrocasts conducted in the Bering Sea. During shallow hydrocasts, measurements and samples are usually taken in the top 200-300m (*i.e.* in the photic layer), while for deep hydrocasts, the entire water-column (*e.g.*

Site/Station number	Latitude (˚N)	Longitude (˚W)	Sample depth (m)	Temperature (˚C)	Salinity	Depth to sea-bed (m)
KS-056	56.64	167.09	surface	10.49	31.82	*ca* .70
KS-057	57.52	167.32	surface	10.08	31.27	*ca* .70
KS-111	58.4	169.96	surface	7.54	31.23	*ca* .70
KS-119	58.04	169.38	surface	7.25	31.33	*ca* .70
KS-120	57.43	168.23	surface	7.07	31.7	*ca* .70
KS-127	57.42	167.34	surface	7.34	31.47	*ca* .70
KS-128	57.38	167.32	surface	7.32	31.48	*ca* .70
KS-129	57.17	167.24	surface	7.63	31.63	*ca* .70
Cocco	57	167.32	surface	10.38	31.45	*ca* .70
St.19	63	167.5	0	7.33 (taken at 1m)	31.39 (taken at 1m)	34
			10	7.26	31.39	
			24	6.89	31.45	
St.31	58.38	170	10	7.28	31.24	70
St.32	57	167.5	0	7.58 (taken at 1m)	31.71 (taken at 1m)	74
			10	7.58	31.71	
			20	7.58	31.71	
			30	7.08	31.76	
			65	3.35	32.27	

Table 1: General information on the underway sites and CTD stations

Station number	Sample depth (m)	Chlorophyll *a* (μg/l)				
		Total	<2μm	2-5μm	5-10μm	>10μm
St.19	0	0.56	0.48	0.03	0.02	0.03
	10	0.49	0.40	0.05	0.02	0.02
	24	2.80	0.45	0.53	0.29	1.53
St.31	10	3.15	0.97	0.73	1.15	0.3
St.32	0	7.13	0.66	0.67	0.74	5.06
	10	7.43	1.12	0.56	0.9	4.85
	20	7.44	1.16	0.54	1.07	4.67
	30	8.44	0.72	0.72	0.56	6.44
	65	0.56	0.05	0.08	0.15	0.28

Table 2: Chlorophyll *a* at the three CTD stations

0-5000m) may be investigated. At each station, a bucket was used to take a surface-water sample. About 2l samples of sea-water were collected in plastic bottles from selected rosette bottles after the CTD rig had returned to the ship. Unlike the underway samples, a more extensive suite of physico-chemical data is available for each CTD station. Of the 76 samples collected in the Bering Sea using this method during this cruise, nine are presently known to contain *Braarudosphaera* coccospheres. These nine samples, taken from various depths, were collected from three hydrocasts, Stations 19, 31 and 32 (see Figure 1, Table 1).

Chlorophyll *a* concentrations were measured, and sorted into four size-fractions: <2μm, 2-5μm, 5-10μm and >10μm (Table 2). Duplicate measurements of nutrient concentrations were made, with values in Table 3 presented as averages.

Water-samples were filtered through Millipore HA-type polycarbonate filters or Advantec mixed cellulose ester filters (47mm diameter, 0.45μm porosity), using an Eyela Aspirator A-3S (Tokyo Rikakikai Co., Ltd.) filtration apparatus, air dried and then stored in plastic petrislides.

A 3 x 3mm portion of each filter was cut out and mounted onto an aluminium stub, coated with platinum/palladium in an Eiko IB-3 ion sputter-coater and examined in a Hitachi S-2250N scanning electron microscope. Photographs were taken with the camera attachment, using Fuji Neopan 120 SS black and white film. Absolute abundances were calculated using the same method as Jordan & Winter (2000).

All of the samples and negatives used in this study are curated in the Department of Earth & Environmental Sciences, Faculty of Science, Yamagata University.

3. Observations

Braarudosphaera bigelowii coccospheres were encountered at three CTD stations and nine underway sampling sites in the shallow waters over the eastern Bering Sea continental shelf. At most of these stations and sites, the surface and subsurface waters were characterised by an *Emiliania huxleyi* bloom (Konno *et al*., in prep.). These waters were relatively cool (7-10°C) and with a low salinity (31-32 PSU), while the environmental dataset from the three CTD stations shows that the *B. bigelowii* coccospheres were present in relatively high-chlorophyll, low-nutrient waters (Tables 1-3). The highest absolute abundances were recorded in the surface-waters at underway sampling sites 'Cocco' (2749 cells/litre) and KS-057 (1394 cells/litre), but significant numbers were also found at KS-056, KS-128 and at 24m and 20m water-depths at CTD Stations 19 and 32, respectively (Table 4).

Two types of *B. bigelowii* coccosphere were recognised, one composed of liths with flat faces (Plate 1) and the other composed of liths with concave faces (Plate 2). Both types were present in relatively low absolute abundances in the Bering Sea (see Table 4), at either the same sampling stations, or at stations in close proximity to each other. Other than the nature of the faces, the two types appear identical. The coccospheres, 13.5-15.3μm in diameter, are regular pentagonal dodecahedrons (*i.e.* with 12 faces) comprising 12 closely-fitting pentaliths (pentagonal coccoliths). Each pentalith, 8.0-9.0μm in length (measured from peak to opposite margin) and with sides 4.7-6.0μm long, is composed of five elements of equal size (3.1-4.0μm in length; the distance between the two parallel sides). The elements are isosceles trapezium in shape (*NB* in American English = isosceles trapezoid). With respect to the shorter of the parallel sides, which is always located at the margin, adjacent elements are rotated by a difference of 72° (as first noted by Deflandre, 1947). Since the corners of such a trapezium would touch the circumference of a circle, the shape could also be referred to as a cyclic quadrilateral. In some specimens, the element-element boundaries within a single pentalith, and also of neighbouring pentaliths, are accentuated by a low ridge (Pl.1, fig.2; Pl.2, fig.6). Usually, there are no gaps between the elements, but occasionally, in concave forms, a star-shaped gap can be seen at the centre of the pentalith (Pl.2, figs 7, 8). Although not shown here, the pentaliths are thick, laminated and distally flare (see proximal views in Nishida & Konda, 1974, pl.IX, fig.58; Tanaka, 1991, pl.4, fig.9).

In addition to the morphological details given above, another fea-

Station number	Sample depth (m)	Average nutrient concentration (μmol/l)			
		Nitrate	Nitrite	Silicate	Phosphate
St.19	0	0.28	0.08	5.54	0.67
	10	0.26	0.07	5.39	0.67
	24	0.35	0.10	6.67	0.74
St.31	10	1.404	0.035	3.293	0.522
St.32	0	1.401	0.04	3.325	0.54
	10	1.404	0.035	3.293	0.522
	20	1.392	0.04	3.284	0.525
	30	10.767	0.209	22.204	1.971
	65	10.754	0.23	22.268	1.976

Table 3: Macronutrient concentrations at the three CTD stations

Site/Station number	Sample depth (m)	Volume filtered (l)	Coccospheres (raw data) Flat type	Concave type	Total (cells/l)
KS-056	surface	3	9	4	518
KS-057	surface	3	26	9	1394
KS-111	surface	2	1		60
KS-119	surface	2	2	1	179
KS-120	surface	2	3		179
KS-127	surface	2	3		179
KS-128	surface	1	4		478
KS-129	surface	2	1		60
Cocco	surface	2	39	7	2749
St.19	0	1		2	239
	10	1		3	359
	24	1		4	478
St.31	10	1	1		120
St.32	0	2	1		60
	10	1	(1)	2(1)	239
	20	1	6		717
	30	1	1		120
	65	2	3		179

() signifies uncertainty of identification

Table 4: Raw data and absolute abundance of *B. bigelowii* coccospheres in the Bering Sea

ture was commonly observed among both types of *Braarudosphaera* coccospheres. Many of the specimens had particles attached to them, arranged along the margins of either the pentaliths or individual pentalith elements (*e.g.* see Pl.1, figs 4, 6; Pl.2, figs 1, 2, 5). These could be bacteria or, given their various shapes and sizes, particles that had merely adhered to the coccoliths. Whatever they are, it is highly likely that their presence is related to organic matter that has been secreted out of the *Braarudosphaera* cell, that is, through potential spaces between abutting coccoliths and plate elements. Alternatively, the particles on the coccolith surface could be blobs of organic matter that were forced out of the cell during filtration or desiccation of the filter onboard the ship.

4. Discussion

4.1 Morphological variation in modern *Braarudosphaera bigelowii*

Takano *et al*. (2006) carried out morphometric studies on cultures of *Braarudosphaera bigelowii* isolated from the Tsugaru Strait, the seaway between the Japanese islands of Hokkaido and Honshu, and showed that it has three size-classes, based on the side length of the pentalith: a small form (<2.4μm), and two intermediate forms, A (4.0-5.3μm) and B (5.3-7.2μm). DNA variation between the latter two forms suggested that they were distinct enough to be regarded as independent species. Gran & Braarud (1935) stated that the coccosphere diameter of their new species, '*Pontosphaera Bigelowi*', was 16μm. Using this measurement, Takano *et al*. (2006) calculated the pentalith side length to be about 6μm (*i.e.* conforming to form B). In general, our specimens also fit into this size-category, although some pentalith side lengths are smaller than 5.3μm (see Figure 2).

The finding of specimens with flat and concave faces is not novel, since Young *et al*. (2003, p.80) had already mentioned this phenomenon. In their original description, Gran & Braarud (1935, p.388) noted that the coccoliths were flat, however, their fig.67 appears to represent a coccosphere with concave faces (compare Pl.2, fig.7 with Figure 3). If so, then the holotype of *B. bigelowii* has concave faces and represents intermediate form B.

Should the two forms (with concave and flat faces) turn out to be separate entities in the future, then the taxonomy of the *B. bigelowii* complex (most fossil pentaliths in Cenozoic sediments are currently assigned to the species) would also need to be reconsidered, since they all appear to bear flat faces. However, for the moment there is not enough evidence to determine whether or not this difference in the nature of the pentalith faces is taxonomically important. But this raises another question. If the two types of face are produced by the same species (given their similar dimensions), what caused the normally flat faces to become concave? Assuming of course that possession of flat faces is 'normal', since, as mentioned above, most illustrated specimens (both living and fossil) bear that type of face. If one considers the methodology used in this study, that is, filtration and air-drying, then it is easy to imagine that, as some of the cells dried, the decreasing cell-volume pulled the pentalith elements inwards. However, why did it only affect some of the coccospheres, as at many of our sites, the nannoplankton assemblages contained both types (see Table 2)? As mentioned above, Gran & Braarud (1935) drew a specimen that had concave faces. This possibly contradicts the desiccation theory, as their specimen was almost certainly preserved and observed in liquid. Thus, the concave morphology may be a natural feature.

Although the presence of attached particles along the lines of the element boundaries is described here for the first time, other workers have shown specimens with the same feature (*e.g.* V. Pariente's specimen at http://www-ocean.tamu.edu/Quarterdeck/QD5.2/b.bigelowi.html). Phytoplankton that leak cellular organic matter are often associated with symbionts or opportunistic organisms. Whilst no conclusive evidence exists for such a relationship in *Braarudosphaera*, it is known to grow in association with Cyanophyceae under certain conditions, for

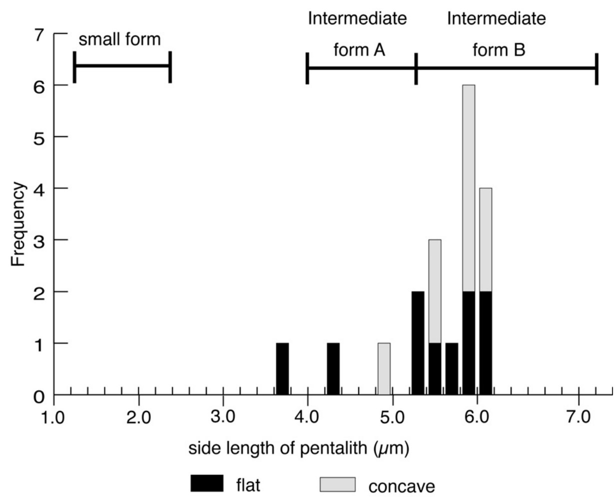


Figure 2: Frequency distribution of pentalith side-lengths of *B. bigelowii* specimens observed in this study (where n = 19; 10 with flat faces, nine with concave faces). Measurements made on coccospheres only. Size-categories taken from Takano *et al*. (2006)

example, in 'l'eau de viviers' (Chrétiennot-Dinet, 1990), which could be translated as man-made ponds used for breeding fish (*i.e*. fish farms).

4.2 Absolute abundances and distribution of modern *Braarudosphaera bigelowii*

In Figure 4, we have plotted all of those sites where living *Braarudosphaera bigelowii* has been recorded. Given the long stratigraphic range of this species 'plexus' in the fossil record (mid-Cretaceous to Present), and the difficulty in separating out modern pentaliths from reworked pentaliths in surface sediments, we have resisted the desire to plot the locations of Recent fossil finds in Figure 4. In this study, living populations of *B. bigelowii* were recorded for the first time in the Bering Sea, albeit in low absolute abundances (up to 10^3 cells/litre). However, these abundances are consistent with those found by most workers in other parts of the world (*e.g*. Smayda, 1966), except for the high concentrations recorded by Duarte-Silva *et al*. (2004). From Figure 4, it appears that our findings (*i.e*. Station 19 in the Bering Sea) represent the highest latitude that living *Braarudosphaera* has been found, although fossil pentaliths from the Lower Oligocene have been reported from ~70˚S (Cape Roberts Project, Ross Sea, Antarctica: S.W. Wise, Jr., pers. comm. to RWJ, 2007).

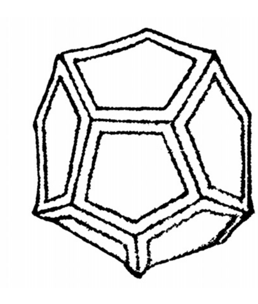


Figure 3: Type illustration of '*Pontosphaera Bigelowi*', reproduced from Gran & Braarud (1935)

4.3 Ecology of *Braarudosphaera bigelowii*

In the literature, *Braarudosphaera bigelowii* is often described as a species living in low-salinity coastal waters, since it is rarely recorded from the open ocean (*e.g*. Sargasso Sea: Gaarder, 1954; Hulburt, 1962). The oceanographic conditions encountered in 2006 suggest that *B. bigelowii* was growing (or entrained) in shallow shelf waters that were relatively cool, with low salinity, and low concentrations of nutrients. Most of the *Braarudosphaera* coccospheres were found in the area affected by an *Emiliania huxleyi* bloom, hence the high concentrations of chlorophyll *a* (although, oddly, the 2-5μm fraction was the lowest of the four categories). Although it may be premature to directly associate *B. bigelowii* with *E. huxleyi* blooms, the situation in 2006 is interesting in many ways. Firstly, the distribution of *B. bigelowii* shown in Figure 4 reveals that many of these locations are also areas where *E. huxleyi* blooms have been reported from. Secondly, the conditions related to these blooms are now widely available in the literature, and so some parallels can be drawn, assuming that the timing of the blooms and the presence of *B. bigelowii* are contemporaneous.

Merico *et al*. (2004) and Lessard *et al*. (2005) reported that *E. huxleyi* can bloom under both high and low nitrate:phosphate ratios, and that the south-eastern Bering Sea was an example of the latter situation. The bloom of 2006 corroborates this, with a N:P ratio of about three (1.5:0.5). Siesser *et al*. (1992) and Kelly *et al*. (2003) invoked upwelling of cool, nutrient-rich intermediate waters to explain the presence of *Braarudosphaera*-rich layers in Lower Oligocene cores. Low-salinity waters and unusual current conditions have also been put forward as a possible cause for past braarudosphaerid blooms (Wise & Kelts, 1972; Bukry, 1974; Siesser *et al*., 1992). Although modern *B. bigelowii* never attains such numbers, unusual weather conditions, high sea-surface temperatures (SSTs), a shallow mixed-layer depth, and high light-saturation levels have been cited as a possible cause of past Bering Sea *E. huxleyi* blooms (Merico *et al*., 2004). The bloom of 2006 occurred in a mixed layer of about 20m, but the SST was only 7˚C. However, it should be noted that the salinity of the Bering Sea during our study was about 31 PSU, a low value for oceanic waters, but perhaps favourable to the growth of *B. bigelowii*, which tends to prefer low-salinity waters.

Clearly, more information is needed to confirm the environmental preferences of *B. bigelowii* and to determine whether it is growing *in situ* with *E. huxleyi* blooms, or is merely entrained in them as a declining relic of an earlier phase, or as a member of a nearshore tychoplankton assemblage carried offshore.

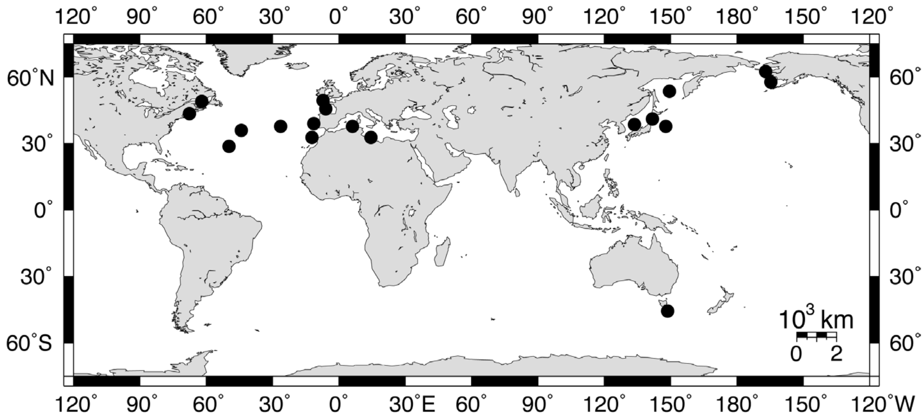


Figure 4: Most of the locations where living *B. bigelowii* has been reported from (including two from sediment trap studies*). Map created using M. Weinelt's 'Online Map Creation' site at www.aquarius.ifm-geomar.de. **Pacific**: Bering Sea (this study), Sea of Okhotsk (*Broerse *et al*., 2000), off and around Japan (Nishida, 1979; Takano *et al*., 2006), south of Tasmania (Hiramatsu & De Deckker, 1996). **Atlantic**: Gulf of Maine and Bay of Fundy (Gran & Braarud, 1935), Gulf of St. Lawrence (Bérard-Therriault *et al*., 1999), Sargasso Sea (Gaarder, 1954; Hulburt, 1962), Roscoff (Lefort, 1972), Bay of Biscay (*Beaufort & Heussner, 2001), English Channel (Boalch, 1987), south of Ireland (Gaarder, 1954), off the Azores (Gaarder, 1954), off Portugal (Duarte-Silva *et al*., 2004), off Atlantic Morocco (Lecal-Schlauder, 1950). **Mediterranean Sea**: off North Africa (Borsetti & Cati, 1972; Knappertsbusch, 1993)

5. Conclusions

In this study, living specimens of *Braarudosphaera bigelowii* were found in the Bering Sea, possibly the highest boreal-latitude occurrence reported so far. The coccospheres exhibited two distinct morphologies, possessing pentaliths with flat or concave faces, and most of the pentalith dimensions correspond to the 'intermediate B' form of Takano *et al*. (2006). The coccospheres of *B. bigelowii* occurred in low abundances and were mostly found in an area associated with a mesoscale bloom of *Emiliania huxleyi*. The hydrographic conditions of this bloom-water generally support the hypothesis that *B. bigelowii* prefers low-salinity, nutrient-rich coastal waters.

Acknowledgements

The authors would like to thank the captain and crew of the *R/V Mirai* and participating scientists for their help in acquiring the samples used in this study. We are also grateful to Catherine Gobin and Stéphane Armand for their help with the French literature. This manuscript has benefited from comments made by Kyoko Hagino, Paul Bown and Jackie Lees.

References

Beaufort, L. & Heussner, S. 2001. Seasonal dynamics of calcareous nannoplankton on a West European continental margin: the Bay of Biscay. *Marine Micropaleontology*, **43**: 27-55.

Bérard-Therriault, L., Poulin, M. & Bossé, L. 1999. Guide d'identification du phytoplancton marin de l'estuaire et du Golfe du Saint-Laurent – incluant également certains protozoaires. *Publication spéciale canadienne des sciences halieutiques et aquatiques*, **128**: 1-387.

Boalch, G.T. 1987. Changes in the phytoplankton of the Western English Channel in recent years. *British Phycological Journal*, **22**(3): 225-235.

Borsetti, A.M. & Cati, F. 1972. Il nannoplancton calcareo vivente nel Tirreno Centro-Meridionale. *Giornale di Geologia*, **38**: 395-452.

Bown, P.R. 2005. Early to Mid-Cretaceous calcareous nannoplankton from the Northwest Pacific Ocean, Leg 198, Shatsky Rise. *In*: T.J. Bralower, I. Premoli Silva & M.J. Malone (Eds). *Proceedings of the ODP, Scientific Results*, **198**: 1-82. Available online at www-odp.tamu.edu/publications/198_SR/VOL-UME/CHAPTERS/103.pdf

Broerse, A.T.C., Ziveri, P. & Honjo, S. 2000. Coccolithophore (-$CaCO_3$) flux in the Sea of Okhotsk: seasonality, settling and alternation processes. *Marine Micropaleontology*, **39**: 179-200.

Bukry, D. 1974. Coccoliths as paleosalinity indicators: evidence from the Black Sea. *AAPG Memoire*, **20**: 335-353.

Burnett, J.A. with contributions from Gallagher, L.T. & Hampton, M.J. 1998. Upper Cretaceous. *In*: P.R. Bown (Ed.). *Calcareous Nannoplankton Biostratigraphy*. British Micropalaeontological Society Publications Series. Chapman & Hall/Kluwer Academic Publishers, London: 132-199.

Chrétiennot-Dinet, M.-J. 1990. Chlorarachniophycées, Chlorophycées, Chrysophycées, Cryptophycées, Euglenophycées, Eustigmatophycées, Prasinophycées, Prymnesiophycées, Rhodophycées, Tribophycées. *Atlas du Phytoplancton Marin*, **3**. Éditions du CNRS.

Cunha, A.A.S. & Shimabukuro, S. 1997. *Braarudosphaera* blooms and anomalous enrichments of *Nannoconus*: evidence from the Turonian South Atlantic, Santos Basin, Brazil. *Journal of Nannoplankton Research*, **19**(1): 51-55.

Deflandre, G. 1947. *Braarudosphaera* nov. gen., type d'une famille nouvelle de Coccolithophoridés actuels à elements composites. *Comptes Rendus Hébdomadaires des Séances de l'Academie des Sciences, Paris*, **225**: 439-441.

Duarte-Silva, A., Palma, S., Sobriho-Goncalves, L. & Moita, M.T. 2004. *Braarudosphaera bigelowii* in waters of the upwelling coast of Portugal. *Journal of Nannoplankton Research*, **26**(2): 35.

Ferreira, J. & Cachão, M. 2005. Calcareous nannoplankton from the Guadiana Estuary and Algarve Continental Shelf (southern Portugal): an ecological model. *Thalassas*, **21**(1): 35-44.

Gaarder, K.R. 1954. Coccolithineae, Silicoflagellatae, Pterospermataceae and other forms from the "Michael Sars" North Atlantic Deep-Sea Expedition 1910. *Report on the*

Scientific Results of the "Michael Sars" North Atlantic Deep-Sea Expedition, 1910, **2**(4): 1-20.

Giunta, S., Morigi, C., Negri, A., Guichard, F. & Lericolais, G. 2007. Holocene biostratigraphy and paleoenvironmental changes in the Black Sea based on calcareous nannoplankton. *Marine Micropaleontology*, **63**(1-2): 91-110.

Gran, H.H. & Braarud, T. 1935. A quantitative study of the phytoplankton in the Bay of Fundy and the Gulf of Maine (including observations on hydrography, chemistry and turbidity). *Journal of the Biological Board of Canada*, **1**(5): 279-467.

Hagino, K. 1997. Distribution of living coccolithophores in the western Pacific Ocean off the coast of Northeast Japan. *Fossil*, **63**: 1-19. (In Japanese)

Hagino, K., Okada, H. & Matsuoka, H. 2000. Spatial dynamics of coccolithophore assemblages in the Equatorial Western-Central Pacific Ocean. *Marine Micropaleontology*, **39**: 53-72.

Hattori, H., Koike, M., Tachikawa, K., Saito, H. & Nagasawa, K. 2004. Spatial variability of living coccolithophore distribution in the western Subarctic Pacific and western Bering Sea. *Journal of Oceanography*, **60**: 505-515.

Heimdal, B.R. 1993. Modern coccolithophorids. *In*: C.R. Tomas (Ed.). *Marine Phytoplankton: A guide to naked flagellates and coccolithophorids*. Academic Press: 147-249.

Heimdal, B.R. & Gaarder, K.R. 1981. Coccolithophorids from the northern part of the eastern central Atlantic. II. Heterococcolithophorids. "*Meteor*" *Forsch-Ergebnisse, Ser. D*, **33**: 37-69.

Hiramatsu, C. & De Deckker, P. 1996. Distribution of calcareous nannoplankton near the Subtropical Convergence, south of Tasmania, Australia. *Marine and Freshwater Research*, **47**: 707-713.

Hulburt, E.M. 1962. Phytoplankton in the southwestern Sargasso Sea and North Equatorial Current, February 1961. *Limnology and Oceanography*, **7**: 307-315.

Hulburt, E.M. & Rodman, J. 1963. Distribution of phytoplankton with respect to salinity between the coast of southern New England and Bermuda. *Limnology and Oceanography*, **8**: 263-269.

Jordan, R.W. & Winter, A. 2000. Assemblages of coccolithophorids and other living microplankton off the coast of Puerto Rico during January-May 1995. *Marine Micropaleontology*, **39**: 113-130.

Kelly, D.C., Norris, R.D. & Zachos, J.C. 2003. Deciphering the paleoceanographic significance of early Oligocene *Braarudosphaera* chalks in the South Atlantic. *Marine Micropaleontology*, **49**: 49-63.

Knappertsbusch, M. 1993. Geographic distribution of living and Holocene coccolithophores in the Mediterranean Sea. *Marine Micropaleontology*, **21**: 219-247.

Lecal-Schlauder, J. 1950. Notes préliminaires sur les Coccolithophorides d'Afrique du Nord. *Société d'Histoire Naturelle d'Afrique du Nord, Bulletin*, **40**: 160-167.

Lefort, F. 1972. Quelques caractères morphologiques de deux espèces actuelles de *Braarudosphaera* (Chrysophycées, Coccolithophoracées). *Botaniste*, **Sér. 55**: 81-93.

Lessard, E.J., Merico, A. & Tyrrell, T. 2005. Nitrate:phosphate ratios and *Emiliania huxleyi* blooms. *Limnology and Oceanography*, **50**(3): 1020-1024.

Martini, E. 1967. Nannoplankton und Umlagerungserscheinungen im Persischen Golf und im nördlichen Arabischen Meer. *Neues Jahrbuch für Geologie und Paläontologie, Monatshefte*, **10**: 597-607.

Merico, A., Tyrrell, T., Lessard, E.J., Oguz, T., Stabeno, P.J., Zeeman, S.I. & Whitledge, T.E. 2004. Modelling phytoplankton succession on the Bering Sea shelf: role of climate influences and trophic interactions in generating *Emiliania huxleyi* blooms 1997-2000. *Deep-Sea Research I*, **51**: 1803-1826.

Nishida, S. 1979. Atlas of Pacific nannoplanktons. *News of Osaka Micropaleontologists, Special Paper*, **3**: 1-31.

Nishida, S. 1981. Nannoplankton biostratigraphy of off Hokuriku and San-in districts, Japan, especially concerned with the stratigraphic meanings of *Coccolithus pelagicus* and *Braarudosphaera bigelowi*. *Chikyu Kankyo*, **35**(4): 204-210. (In Japanese)

Nishida, S. & Konda, I. 1974. Planktonic foraminifera and calcareous nannoplankton in the bottom samples obtained from off the Kii Peninsula and Shikoku Island, Japan. *Bulletin of Nara University of Education*, **23**, 2 (Natural Science): 51-91. (In Japanese)

Nishitani, H. & Zhang, J. 2005. The phytoplankton distribution and its variation linked with marine environment changes – *Emiliania huxleyi* bloom mechanism in the southeastern Bering Sea shelf. *Kaiyo Monthly*, **39**: 178-185. (In Japanese)

Okada, H. & Honjo, S. 1973. The distribution of ocean coccolithophorids in the Pacific. *Deep-Sea Research*, **20**: 335-374.

Olson, M.B. & Strom, S.L. 2002. Phytoplankton growth, microzooplankton herbivory and community structure in the southeast Bering Sea: insight into the formation and temporal persistence of an *Emiliania huxleyi* bloom. *Deep-Sea Research II*, **49**: 5969-5990.

Parker, M.E., Clark, M. & Wise, S.W., Jr. 1985. Calcareous nannofossils of Deep Sea Drilling Project Sites 558 and 563, North Atlantic Ocean: biostratigraphy and the distribution of Oligocene braarudosphaerids. *In*: H. Bougault, S.C. Cande *et al*. (Eds). *Initial Reports of the DSDP*, **82**: 559-589.

Peleo-Alampay, A.M., Mead, G.A. & Wei, W. 1999. Unusual Oligocene *Braarudosphaera*-rich layers of the South Atlantic and their palaeoceanographic implications. *Journal of Nannoplankton Research*, **21**(1): 17-26.

Reid, F.M.H. 1980. Coccolithophorids of the North Pacific Central Gyre with notes on their vertical and seasonal distribution. *Micropaleontology*, **26**: 151-176.

Scholle, P.A. & Kling, S.A. 1972. Southern British Honduras: lagoonal coccolith ooze. *Journal of Sedimentary Petrology*, **42**: 195-204.

Shin, K.-H., Tanaka, N., Harada, N. & Marty, J.-C. 2002. Production and turnover rates of C_{37} alkenones in the eastern Bering Sea: implication for the mechanism of a long duration of *Emiliania huxleyi* bloom. *Progress in Oceanography*, **55**: 113-129.

Siesser, W.G., Bralower, T.J. & De Carlo, E.H. 1992. Mid-Tertiary *Braarudosphaera*-rich sediments on the Exmouth Plateau. *Proceedings of the ODP, Scientific Results*, **122**: 653-663.

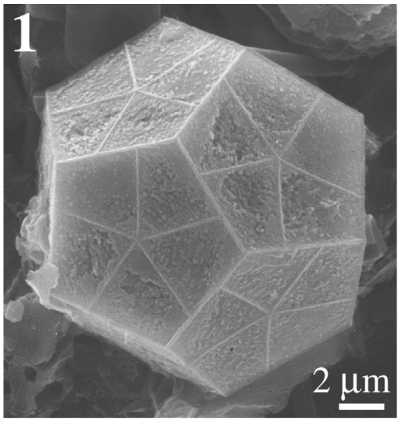
Smayda, T.J. 1966. A quantitative analysis of the ecological conditions and the phytoplankton dynamics at 8°45'N, 79°23'W from November 1954 to May 1957. *Inter-American Tropical Tuna Commission Bulletin*, **II**: 353-612.

Stockwell, D.A., Whitledge, T.E., Zeeman, S.I., Coyle, K.O., Napp, J.M., Brodeur, R.D., Pinchuk, A.I. & Hunt, G.L., Jr. 2001. Anomalous conditions in the south-eastern Bering Sea, 1997. *Fisheries Oceanography*, **10**: 99-116.

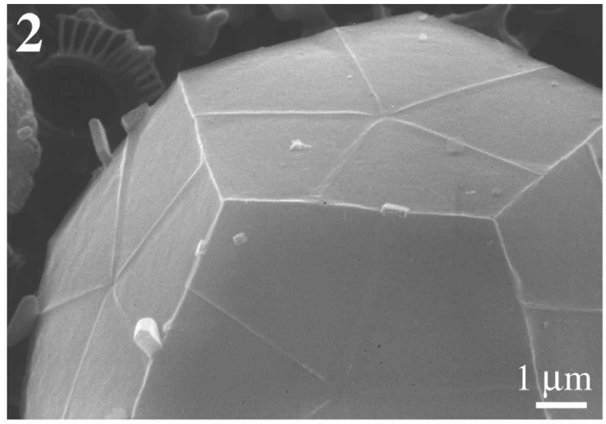
Sukhanova, I.N. & Flint, M.V. 1998. Anomalous blooming of

Plate 1

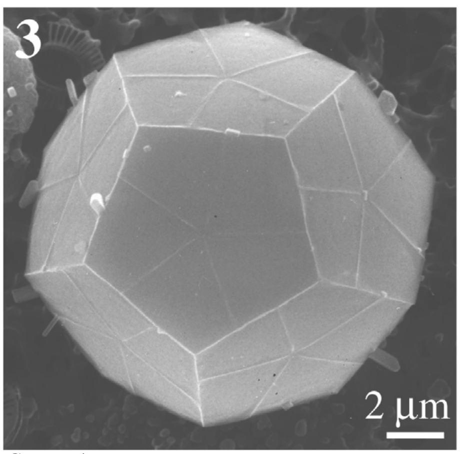
Braarudosphaera bigelowii flat form



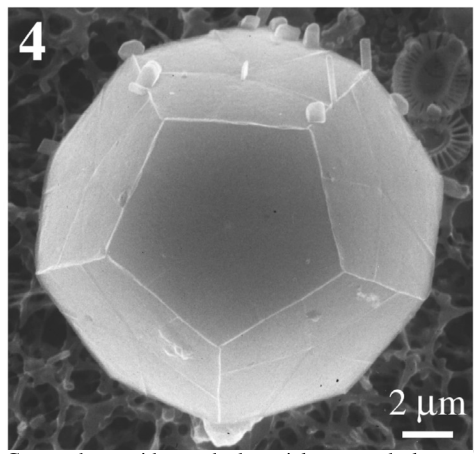
Coccosphere with etched surface
Bering Sea, St.32 (65m)



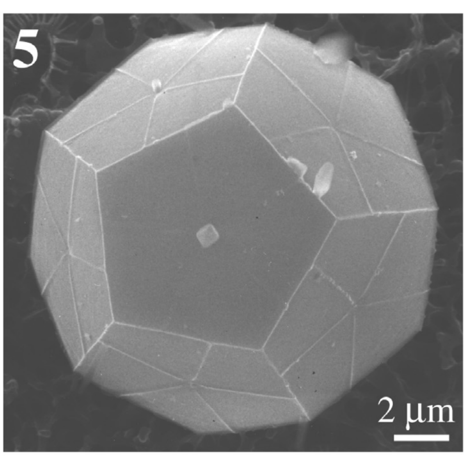
High magnification of specimen in Fig.3. Note ridge at element margins
Bering Sea, KS-057



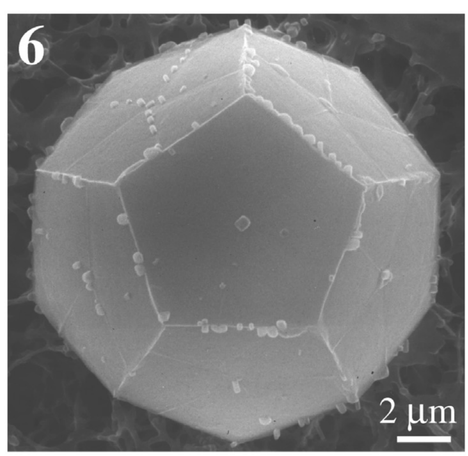
Coccosphere
Bering Sea, KS-057



Coccosphere with attached particles around element margin
Bering Sea, KS-057



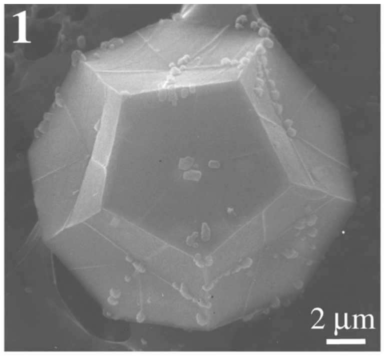
Coccosphere
Bering Sea, KS-057



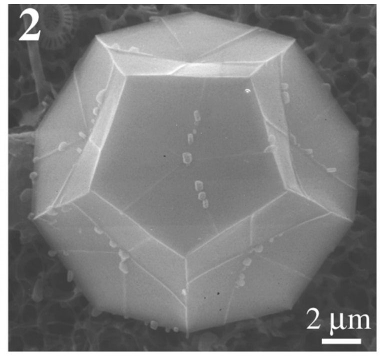
Coccosphere with attached particles around element margins
Bering Sea, KS-057

Plate 2

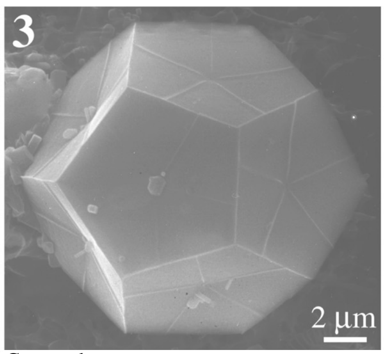
Braarudosphaera bigelowii concave form



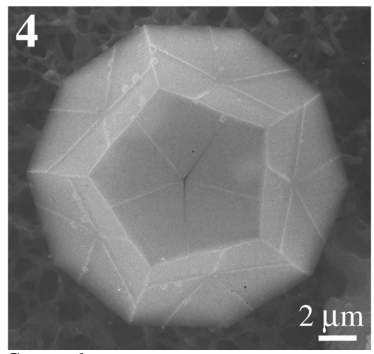
Coccosphere with attached particles around element margins
Bering Sea, KS-057



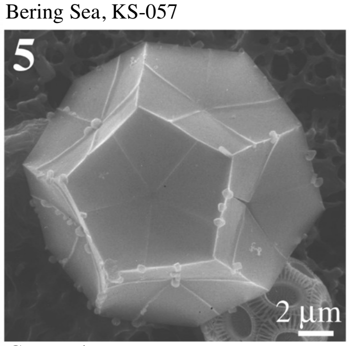
Coccosphere with attached particles around element margins
Bering Sea, KS-057



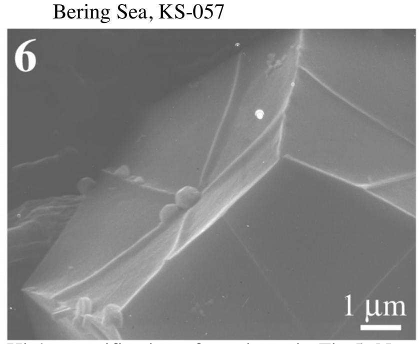
Coccosphere
Bering Sea, KS-057



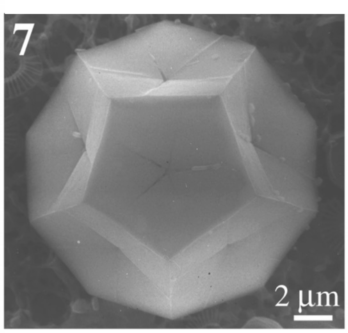
Coccosphere
Bering Sea, KS-057



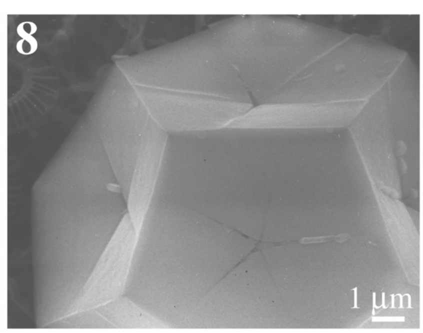
Coccosphere
Bering Sea, KS-057



High magnification of specimen in Fig.5. Note ridge at element margins
Bering Sea, KS-057



Coccosphere
Bering Sea, KS-057



High magnification of specimen in Fig.7. Note prominent star-shaped gap in central area
Bering Sea, KS-057

coccolithophorids over the eastern Bering Sea shelf. *Oceanology*, **38**(4): 502-505.

Svábenická, L. 1999. *Braarudosphaera*-rich sediments in the Turonian of the Bohemian Cretaceous Basin, Czech Republic. *Cretaceous Research*, **20**: 773-782.

Takahashi, K., Fujitani, N. & Yanada, M. 2002. Long term monitoring of particle fluxes in the Bering Sea and the central subarctic Pacific Ocean, 1990-2000. *Progress in Oceanography*, **55**: 95-112.

Takahashi, K. & Okada, H. 2000. Environmental control on the biogeography of modern coccolithophores in the southeastern Indian Ocean offshore of Western Australia. *Marine Micropaleontology*, **39**: 73-86.

Takano, Y., Hagino, K., Tanaka, Y., Horiguchi, T. & Okada, H. 2006. Phylogenetic affinities of an enigmatic nannoplankton, *Braarudosphaera bigelowii*, based on the SSU rDNA sequences. *Marine Micropaleontology*, **60**(2): 145-156.

Takayama, T. 1972. A note on the distribution of *Braarudosphaera bigelowi* (Gran and Braarud) Deflandre in the bottom sediments of Sendai Bay, Japan. *Transactions of the Proceedings of the Palaeontological Society of Japan, N.S.*, **87**: 429-435.

Tanaka, Y. 1991. Calcareous nannoplankton thanatocoenoses in surface sediments from seas around Japan. *Science Reports of the Tohoku University, Sendai, Second Series (Geology)*, **61**(2): 127-198.

Tanimoto, M., Aizawa, C. & Jordan, R.W. 2003. Assemblages of living microplankton from the subarctic North Pacific and Bering Sea during July-August 1999. *Courier Forschungsinstitut Senckenberg*, **244**: 83-103.

Vance, T.C., Schumacher, J.D., Stabeno, P.J., Baier, C.T., Wyllie-Echeverria, T., Tynan, C.T., Brodeur, R.D., Napp, J.M., Coyle, K.O., Decker, M.B., Hunt, G.L., Stockwell, D., Whitledge, T.E., Jump, M. & Zeeman, S. 1998. Aquamarine waters recorded for the first time in eastern Bering Sea. *EOS, Transactions, American Geophysical Union*, **79**(10): 121-126.

Wise, S.W., Jr. & Kelts, K.R. 1972. Inferred diagenetic history of a weakly silicified deep sea chalk. *Transactions of the Gulf Coast Association of Geological Societies*, **22**: 177-302.

Young, J.R., Geisen, M., Cros, L., Kleijne, A., Sprengel, C., Probert, I. & Østergaard, J. 2003. A guide to extant coccolithophore taxonomy. *Journal of Nannoplankton Research, Special Issue* **1**: 1-125.

Zhang, J. & Siesser, W.G. 1986. Calcareous nannoplankton in continental-shelf sediments, East China Sea. *Micropaleontology*, **32**: 271-281.

Appendix

List of taxa mentioned in the text, with their authorities.

Braarudosphaera Deflandre
Braarudosphaera bigelowii (Gran & Braarud) Deflandre
Braarudosphaera deflandrei Lecal
Coccolithus pelagicus (Wallich) Schiller
Emiliania huxleyi (Lohmann) Hay & Mohler
Micrantholithus Deflandre