**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**
*Beraurudosphaera* 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 braarudosphaerid 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; Sväbenická, 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 & Catì, 1972; Knappertsbusch, 1993), off eastern North America (Gran & Braarud, 1935; Bérard-Therriault et al., 1999), in the Sargasso Sea (Gaarder, 1954; Hulbert, 1962; Hulbert & 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., 2004), and in the North Pacific (Nishida, 1979). It should be noted that *Braarudosphaera bigelowii* has also been
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 10³ 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.

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

Table 1: General information on the underway sites and CTD stations
Absolute abundances were calculated using the same method, using Fuji Neopan 120 SS black and white film. Photographs were taken with the camera attached in a Hitachi S-2250N scanning electron microscope. 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. The elements, but occasionally, in concave forms, a star-shaped gap can be seen at the centre of the pentalith (Plate 1, fig.2; Plate 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-
Table 4: Raw data and absolute abundance of *B. bigelowii* coccospheres in the Bering Sea

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

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

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 Bigelovii*, 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 nanoplankton 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 symbions 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
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).

**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; Hulbert, 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 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)

**Figure 3**: Type illustration of ‘*Pontosphaera Bigelowi*’, reproduced from Gran & Braarud (1935)
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 pentahalites with flat or concave faces, and most of the pentahalite 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


Plate 1

*Braarudosphaera bigelowii* flat form

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

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

3. Coccoosphere
   Bering Sea, KS-057

4. Coccoosphere with attached particles around element margin
   Bering Sea, KS-057

5. Coccoosphere
   Bering Sea, KS-057

6. Coccoosphere 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

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

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


**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