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ECOLOGY

Diatom assemblages on Nanaura mudflat, Ariake Sea, Japan: with reference to the biogeography of marine benthic diatoms in Northeast Asia

Jinsoon PARK[1], Jong Seong KHIM[1,]*, Taisuke OHTSUKA[2], Hiroyuki ARAKI[3], Andrzej WITKOWSKI[4], and Chul-Hwan KOH[5,]*

[1]*Division of Environmental Science and Ecological Engineering, Korea University, Seoul 136-713, Republic of Korea*
[2]*Lake Biwa Museum, Oroshimo 1091, Kusatsu, Shiga 525-0001, Japan*
[3]*Institute of Lowland Technology, Saga University, Saga 840-8502, Japan*
[4]*Department of Paleooceanology, Institute of Marine Sciences, University of Szczecin, Waska 13, PL-71-415 Szczecin, Poland*
[5]*School of Earth and Environmental Sciences (Oceanography), Seoul National University, Seoul 151-742, Republic of Korea*

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ABSTRACT. A study was conducted to understand the floral characteristics and diversity of benthic diatoms (Bacillariophyceae) at Nanaura mudflat (E 130° 10′, N 33° 04′) on the coast of the Ariake Sea, Japan. A literature review was also performed to better understand the biogeography of the marine benthic diatoms of Northeast Asia. Light microscopic and scanning electron microscopic observations revealed a total of 90 Nanaura taxa. All species were listed along with their dimensions, microstructural densities, and if necessary, their ultrastructures. Dominant species found were *Navicula* sp. 1 (12.6%), *Paralia sulcata* (10.3%), *Tryblionella granulata* (8.8%), *Navicula flantanica* (6.8%), *Gyrosigma wansbeckii* (5.8%) and *Cyclotella striata* (5.6%). The abundance of the six species collectively accounted for ca. 50% of the total. As for salinity requirements, marine and brackish-marine forms were dominant, while brackish and freshwater species were also observed. Species composition of diatom flora at the study site showed relatively close similarity with those of mudflat (e.g., Isahaya Bay) and brackish lagoon (Matsukawaura Lagoon) in Japan, but were also similar to those of other localities, e.g. at Songdo mudflat in Korea and Fujian coast in China. Thirteen reports of the benthic diatoms from Northeast Asia were selected for comparison based on diatom habitats and data quality. Twenty-one species of Nanaura diatoms, including *Cymatotheca weissflogii* and *Tryblioptychus cocconeiformis,* whose reports are rare in the Western Hemisphere and Europe, occurred across Japan, Korea, and China, and represent common benthic diatoms in Northeast Asia.

Keywords: Biogeography; Diatom flora; Japan; Mudflat; Northeast Asia.

INTRODUCTION

The tidal flats along the Ariake Sea coast of Japan are not only well known for their large surface area (ca. 200 km^2, or about 40% of the total area covered by tidal flats in Japan), (Araki et al., 2001), but also for the anti-conservation Isahaya Bay reclamation project. Many studies have been carried out to assess and monitor the Ariake Sea ecosystem as a result of local concern. One of the studies was looking for benthic diatom communities in Isahaya, Ariake Sea (Ohtsuka, 2005), however, the study focused mainly on taxonomic description rather than ecological perspectives. While studies of benthic diatoms are of great concern and importance in tidal flat ecosystems, only a few studies in Japan have addressed their ecological implications, such as in benthic-pelagic coupling (Hirose et al., 2004; Koh et al., 2006; Koh et al., 2007).

Apart from Japanese tidal flats, the most typical tidal flats are those of the Yellow Sea in Northeast Asia, which are widely developed along the east coast of China and the west to south coasts of Korea, where studies of marine benthic diatoms are also lacking. Diatom study efforts in Northeast Asia are underestimated, however, due to lack of international exposure, particularly from China. Meanwhile, a geographical distribution study of benthic diatoms in Japan, Korea, and China would be of great benefit, and provide a better understanding of the benthic flora biogeography of Northeast Asia. Since a limited number of re-

*Corresponding author: J.S. Khim & C.H. Koh Correspondence and requests for materials during the remaining review process would be kindly requested to Prof. J. S. Khim at E-mail: jongseongkhim@korea.ac.kr; Tel: ++82-2-3290-3041; Fax: ++82-2-953-0737.

ports are available on marine benthic diatoms in the three countries listed above, all available literature (n=34) from Northeast Asia encompassing tidal flat or coastal (n=6), as well as other benthic environments, such as estuary (n=5), lake (n=7), river (n=6), and others (n=10), are included for comparison.

The nomenclature and flora established in Europe and North America have long been adopted and applied to floristic and taxonomic studies on benthic diatoms in Asian countries. Using this approach, the taxa identified in the region were considered cosmopolitan. While few endemic forms were reported, their high occurrence in such unexplored habitats was expected. Thus, the correct identification of benthic diatoms in our materials and of other samples from Northeast Asia, is vital for floristic and taxonomic studies, especially for comparative studies. Comparisons based solely on checklists are misleading, and photographic documentation and morphological information should be addressed as far as possible. In the present study, those species likely misidentified and/or in question among the reviewed literature were carefully reevaluated. Alternative identifications were suggested accordingly and used for regional comparisons before larger comparisons were made.

Dominant species in Northeast Asian tidal flats seem to be different from their European and North American counterparts, judging from previous reports as well as personal observations. For example, often missing in Korea and Japan are large motile species representing genera of e.g. *Navicula*, *Nitzschia*, *Bacillaria*, *Cylindrotheca*, *Gyrosigma*, *Pleurosigma*, and *Surirella* (Hustedt, 1939, 1955, 1959; Brockmann, 1950; Hendey, 1964; Underwood, 1994; Witkowski et al., 2004), which often dominate European tidal flats. While the predominant species in Northeast Asia, accepting that data is limited, are reported as a large *Haslea* species (*H. nipkowii*) from a Japanese mudflat (Othsuka, 2005) and *Fogedia* and *Navicula* (personal data) from the Korean sand flat. To better understand their floral characteristics in terms of biogeography, we first tried to extract the typical and common species in Japan (Nanaura), Korea (Songdo), and China (Fujian), then address their global distribution.

In brief, the present study aimed to: 1) report the diatom flora of the Nanaura mudflat, Ariake Sea, along with each species' relative abundance and dimensional and microstructural information based on light microscopic (LM) and scanning electron microscopic (SEM) observations; 2) examine and compare concurrently occurring species between Nanaura mudflat and Northeast Asia and their biogeographic distribution; and 3) extract and address the global distribution of typical and/or common Northeast Asian species.

MATERIALS AND METHODS

Sampling and observation

The top 0-0.5 cm of surface sediment was collected from the uppermost tidal flat during ebb tide at Nanaura (E 130° 10′, N 33° 04′), Ariake Sea, Japan, on Oct. 2002 (Figure 1). Permanent slide cleaning and preparation involved a concentrated HCl and H_2O_2 treatment to remove calcium carbonate particles in the sediment and organic materials in the cells. Permanent slides were made using pleurax mountant. The specimens were then photographed under the Olympus BX60 LM with ×60 Plan Apo objective lens, Zeiss Axioscop LM with ×100 Achromat objective lens, and JEOL 6301F SEM (Figure 4). Under the LM observation (Figures 5-8), ca. 1,000 valves were counted and the relative abundance of each taxon was calculated.

Figure 1. Map showing the study area and 11 other benthic habitats in Northeast Asia from which diatom flora literature were reviewed. A-D (●): coastal and mudflat environments; A: Nanaura mudflat (this study); B: Gyeonggi Bay (Choi, 1988; Noh et al., 2001); C: Fujian coast (Jin et al., 1985, 1991); D: Isahaya Bay (Ohtsuka, 2005); E-H (●): brackish water environments; E: Matsukawaura Lagoon (Nigorikawa and Hasegawa, 1999); F: Kase River Estuary (Yamakawa, 1994); G: Lake Kamo (Hasegawa and Nigorikawa, 1993); H: Nakdong River Estuary (Cho, 1988); I-L (○): freshwater environments; I: Yungchun Dam Reservoir (Lee et al., 1992); J: Hii River (Ohtsuka, 2002); K: Inagawa River (Houki, 1986); L: Lake Biwa (Watanabe and Houki, 1988).

Literature survey

A literature survey followed by comparative analysis were performed to gain a better understanding of the floral characteristics of Nanaura diatoms. Of major interest herein was to delineate the regional and habitual distribution of Nanaura diatoms across the various benthic habitats in Northeast Asia.

Diatom taxa identified to the species level only (n=77) were considered for the analysis. First, we collected all

Table 1. List of literatures of the benthic diatom studies (n = 34) conducted in Northeast Asia. For a comparison with diatom flora from the Nanaura mudflat, Japan, literatures were selected based on the following criteria, considering: 1) benthic habitat (whether it deals with representative benthic habitat), 2) number of concurrently occurred species. (this study vs. other studies), 3) percent of the species with photographs (realtive to total reported), and 4) salinity range (whether salinity clearly reported as one of marine, brackish or fresh environment). Total of 13 literatures representing 11 benthic habitats are selected and used for cluster analysis (see Table 2).

Sampling			Criteria (with evaluation: ○, Δ, ×)					Reference(s)	
Materials	Site	Country	1) Habitat	2) Number of concurrentry occurred species	3) Percent species with photographs	4) Salinity	Overall	Author(s)	Year
A) Marine									
Mud, etc.	Fujian coast, etc.	China	mudflat etc (○)	31 (○)	~90% (○)	marine (○)	selected	Jin et al.	1985; 1991
Mud	Songdo mudflat Gyeonggi Bay	Korea	mudflat (○)	34 (○)	100% (○)	marine (○)	selected	Choi; Noh et al.	1988; 2001
Sediment	Osaka Bay Osaka	Japan	bay sediment (Δ)	21 (○)	31% (×)	marine (○)	×	Hirose et al.	2004
Mud	Isahaya mudflat Nagasaki	Japan	mudflat (○)	26 (○)	15%a (○)	marine (○)	selected	Ohtsuka	2005
B) Brackish									
Stone, etc.	Yodo River Osaka	Japan	upper estuary (Δ)	4 (×)	62% (Δ)	brackish (○)	×	Gotoh	1978
Stone, etc.	Yodo River Estuary Osaka	Japan	estuary (○)	1 (×)	24% (×)	brackish (○)	×	Gotoh	1979
Stone, etc.	Kumano-gawa River Estuary	Japan	estuary (○)	3 (×)	60% (Δ)	nearly fresh (×)	×	Gotoh	1986
Sediment	Nakdong River Estuary Gyeongnam	Korea	estuary (○)	8 (Δ)	100% (○)	brackish (○)	selected	Cho	1988
Ooze, etc.	Lake Kamo Niigata	Japan	lake (saline) (○)	11 (○)	67% (○)	brackish (○)	selected	Hasegawa & Nigorikawa	1993
Stone	Kasa River Esturay Saga	Japan	estuary (○)	16 (○)	100% (○)	brackish (○)	selected	Yamakawa	1994
Ooze	Matsukawaura Lagoon Fukushima	Japan	lagoon (○)	20 (○)	60% (Δ)	brackish (○)	selected	Nigorikawa & Hasegawa	1999
Sand	Bukcheong River Hamgyeongnamdo	Korea	river (○)	3 (×)	89% (○)	brackish (○)	×	Cho	2000a
Water plant	Guemho Lakes Hamgyeongnamdo	Korea	lake (○)	5 (Δ)	76% (○)	nearly fresh (×)	×	Cho	2000b
Ooze, etc.	Mikatagoko Lakes Fukui	Japan	lake (○)	8 (Δ)	NAb	fresh & brackish (×)	×	Nigorikawa & Hasegawa	2000
Concrete and Stone	Mine & Katase Spa Honshu	Japan	spa (×)	0 (×)	100% (○)	nearly fresh (×)	×	Shinohara et al.	2001
Dead cells from the lake bottom	Lake Takahoko Aomori	Japan	thanatocenosis (×)	9 (Δ)	45% (Δ)	brackish (○)	×	Nigorikawa & Hasegawa	2002

Table 1. (Continued)

Sampling			Criteria (with evaluation: ○, Δ, ×)					Reference(s)	
Materials	Site	Country	1) Habitat	2) Number of concurrentry occurred species	3) Percent species with photographs	4) Salinity	Overall	Author(s)	Year
Stone	Ito & Yugawara Spa Honshu	Japan	spa (×)	1 (×)	100% (○)	nearly fresh (×)	×	Shinohara & Fukushima	2002
C) Freshwater									
Stone	Ina-gawa River Hyogo/Osaka	Japan	river (○)	5 (Δ)	66% (Δ)	fresh (○)	selected	Houki	1986
Sedimentc	Paddy fields Nara	Japan	paddy field (×)	3 (×)	30% (×)	fresh (○)	×	Negoro & Higashino	1986
Stone	Local Springs Okinawa	Japan	spring (×)	2 (×)	48% (Δ)	fresh (○)	×	Nakai	1987
Stone, etc.	Lake Biwa Shiga	Japan	lake (○)	5 (Δ)	70% (○)	fresh (○)	selected	Watanabe & Houki	1988
Stone	Lake Mashu Hokkaido	Japan	lake (○)	1 (×)	100% (○)	fresh (○)	×	Watanabe	1990
Soil and Moss	Nine locations Honshu	Japna	soil/moss (×)	1 (×)	100% (○)	fresh (○)	×	Ito & Horiuchi	1991
Stone, etc.	Yuncheon Dam Gyeongbuk	Korea	reservoir and river (○)	7 (Δ)	100% (○)	fresh (○)	selected	Lee et al.	1992
Stone	Kwang River Gyeongbuk	Korea	river (○)	7 (Δ)	45% (Δ)	fresh to marine (×)	×	Lee et al.	1994a; 1994b
Stone	Local Spa Shikawa	Japan	alkaline hot spring (×)	1 (×)	100% (○)	fresh (○)	×	Watanabe & Asai	1995
Mud	Lake Nojiri Nagano	Japan	lake (○)	5 (Δ)	9% (×)	fresh (○)	×	Haraguchi	1999
Water plant	Sugao Swamp Ibaragi	Japan	swamp (Δ)	7 (Δ)	7% (×)	fresh (○)	×	Haraguchi	2000
Mud	Lake Yogo Shiga	Japan	lake (○)	5 (Δ)	7% (×)	fresh (○)	×	Haraguchi	2001
Soil	Paddy fields Kyoto	Japan	paddy field (×)	5 (Δ)	100% (○)	fresh (○)	×	Ohtsuka	2001
Stone, Sand, Mud	Hii River Shimane	Japan	river (○)	5 (Δ)	100% (○)	fresh (○)	selected	Ohtsuka	2002

[a]Photographs not fully provided in the paper, but available through persnonal communication with the author (Ohtsuka).
[b]NA: not applicable because the authors provided the list of 'representative species' only.
[c]Material not specified in the paper, yet presumed as sediment considering that the study site was a paddy field.

available literature (n=34) on benthic diatom floristic studies reported in Northeast Asia (Table 1). Reports on benthic diatoms from brackish and freshwaters were also included for analysis, as many species from Nanaura mudflat are not likely typical marine. Literature selections were made, for comparative purposes, based on the following criteria; 1) whether the study dealt with representative benthic habitats, 2) whether the number of concurrently occurred species (present vs. other studies) was relevant, 3) whether the percentage of species with photographs (relative to total reported) is comparable enough (>33.3%) between studies, and finally 4) whether salinity is clearly given as marine, brackish, or fresh environment. Each criterion was evaluated and scored as good (○ = 1.0), acceptable (Δ = 0.5), or inappropriate (× = 0) and those without an '×' and with a summed score ≥ 3 were selected for analysis.

Cluster analysis

Of 34 floristic studies for Northeast Asia, a total of 13 (7 in Japan, 4 in Korea, and 2 in China), representing 11 benthic habitats, were finally selected, after which cluster analysis was performed. First, Nanaura species (n=77) were listed alphabetically as "objectives" in the cluster analysis matrix. Twelve habitats (Nanaura mudflat + 11 selected localities) were then arranged as variables of the matrix shown in Table 3. Secondly, the occurrence of corresponding species in each habitat was given as '+1 (occurred)' and '0 (absent)', respectively. In the meantime, warranting the data quality, a few species of questionable identity in the corresponding literature(s) were re-identified based on original and/or authoritative literature (Table 4). Finally, the meta-data (viz. 12×77 matrix) was computed using Multivariate Statistical Package (MVSP – Kovach Computing Services, 1993). The cluster analysis employed the minimum variance method. Squared Euclidian Distance was adopted as dissimilarity index. The resulting dendrogram is presented in Figure 2.

RESULTS

Species composition and abundance of Nanaura diatoms

In total, 90 diatom taxa from Nanaura mudflat were observed. Table 2 shows the list of species with their dimensions and microstructural densities. Overall, benthic

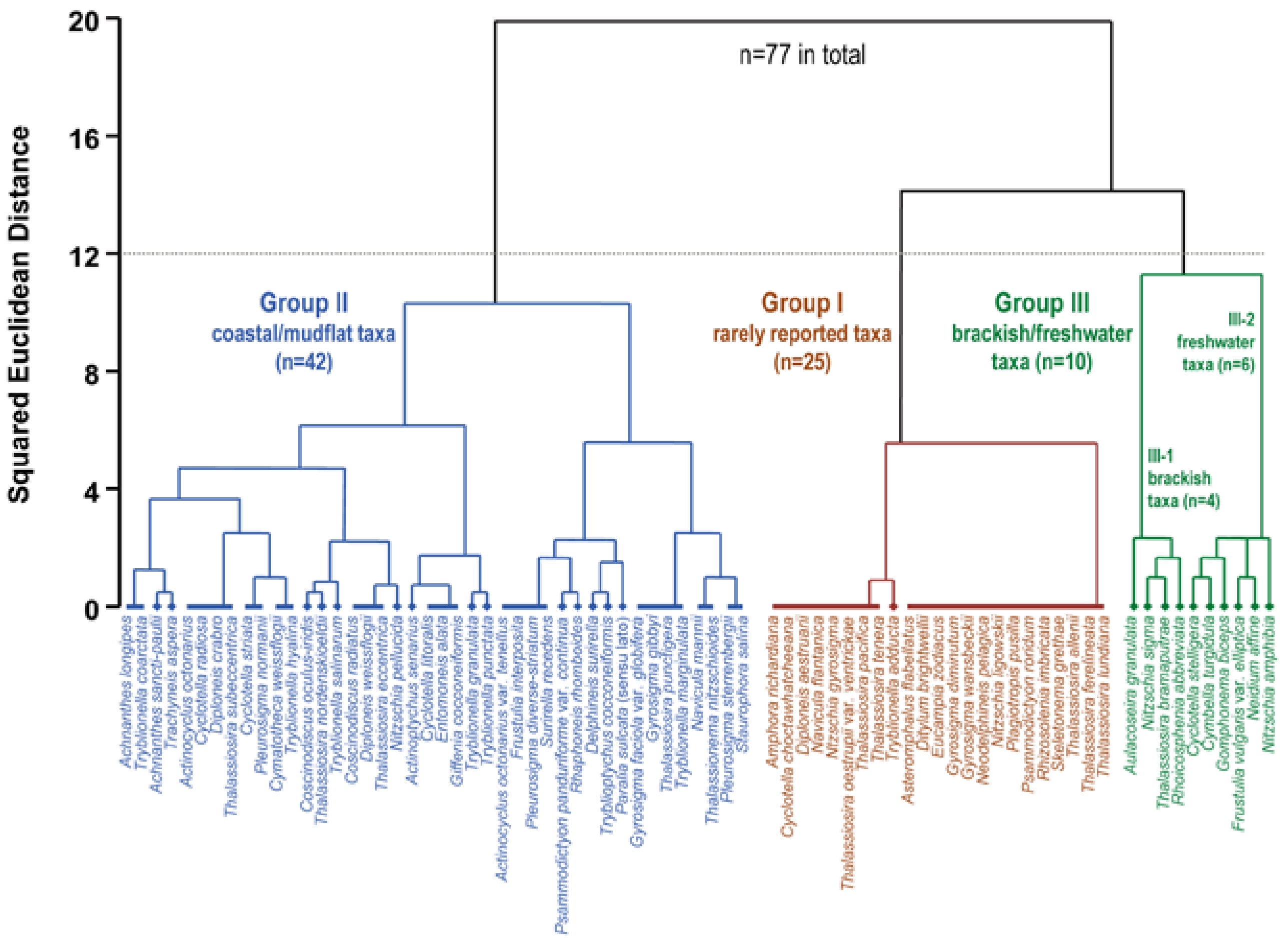

Figure 2. Dendrogram by cluster analysis for the 77 Nanaura diatoms, where corresponding taxa are clearly identified to the species level. The value of the dissimilarity index (Squared Euclidian Distance) applied was 12, and Nanaura diatoms are divided into three groups; Group I (rarely reported taxa), Group II (coastal and mudflat taxa), and Group III (brackish and freshwater taxa).

Table 2. List of diatom taxa observed in Nanaura mudflat. Relative abundance, dimensional information and density of microstructures were presented as well.

Species	Relative abundance (%)	Dimension in mm		Density of microstructures in 10 mm
		Diameter	Length/ Width	Areaolae (A), Costae (C), Fibulae (F), Longitudinal Striae (LS), Marginal Processes (MP), Oblique Striae (OS), Striae (S), Transapical Ribs (TR) and Transapical Striae (TS)
Centric Diatoms				
Actinocyclus octonarius	0.1	45-60		A: 10
Actinocyclus octonarius var. *tenellus*	0.1	39-41		A: 8-9
Actinoptychus senarius	0.7	3-42		
Asteromphalus flabellatus	0.1		38-44/29-33	A: 15
Aulacoseira granulata	0.2	5		A: 16 (on valve mantle)
Coscinodiscus oculus-iridis	0.1	153		A: 4-5; MP: 2
Coscinodiscus radiatus	0.2	65-68		A: 4-6
Cyclotella choctawhatcheeana	2.2	8.5-10		S: 18 (at the margin)
Cyclotella litoralis	3.8	13-17		S: 13 (at the margin)
Cyclotella radiosa	0.2	9-19		S: 15 (at the margin)
Cyclotella stelligera	0.1	9		S: 12 (at the margin)
Cyclotella striata	5.6	15-30		S: 8-9 (at the margin)
Cymatotheca weissflogii	2.9		13-17/12-15	A: 11
Ditylum brightwellii	0.1	33		A: ~10
Eucampia zodiacus	0.1	57		A: 13
Paralia sulcata	10.3	9-23		S: 12 (at the margin)
Rhizosolenia imbricata	0.1	25		A: 20 (on valve mantle)
Skeletonema grethae	1.6	7.5-10		A: ~30
Thalassiosira allenii	1.9	8		A: 24; MP: 5
Thalassiosira bramaputrae	1.6	15-25		A: 20
Thalassiosira eccentrica	1.2	17-28		A: 7-8 at the valve center, 9 near the valve margin
Thalassiosira eccentrica var. *fasciculata*	0.4	29-34		A: 10 at the valve center, 12 near the valve margin; MP: 4
Thalassiosira ferelineata	1.2	18-23		A: 6-7
Thalassiosira lundiana	0.1	20		A: 30; MP: 12
Thalassiosira nordenskioeldii	0.3	22		A: 15-18; MP 2.5
Thalassiosira oestrupii var. *ventrickae*	1.1	12-17		A: 9-10 at the valve center, 12 near the valve margin
Thalassiosira pacifica	0.3	23		A: 13; MP: 6
Thalassiosira punctigera	0.1	53		A: 15-18; MP: 4
Thalassiosira tenera	1.1	11-20		A: 9; MP: 5
Tryblioptychus cocconeiformis	0.7		19-27/17-25	S: 9
Araphid Diatoms				
Delphineis surirella	0.1		13-27/8-14	A: ~9; TS: 8
Neodelphineis pelagica	0.4		15-21/4.5-5	TS: 14
Rhaphoneis rhomboides	0.2		25/14	A: 10; TS: 10
Thalassionema nitzschioides	1.9		30-49/3	A: 12
Raphid Diatoms				
Achnanthes longipes	0.2		31-43/9.5-12	TS: 15

Table 2. (Continued)

Species	Relative abundance (%)	Dimension in mm		Density of microstructures in 10 mm
		Diameter	Length/ Width	Areaolae (A), Costae (C), Fibulae (F), Longitudinal Striae (LS), Marginal Processes (MP), Oblique Striae (OS), Striae (S), Transapical Ribs (TR) and Transapical Striae (TS)
Achnanthes cf. *pseudogroenlandica*	0.1		30-35/6	TS: 12 in RV, 9 in RLV
Achnanthes sancti-paulii	0.1		35/19	A: 11; TS: 7
Amphora richardiana	0.1		29-33/7-7.5	A: ~15; S: 12 at the dorsal side, 18 at the ventral side
Cymbella turgidula	0.1		31/11	A: 24; TS: 9
Diploneis aestruarii	0.1		18-21/7.5	TS: 15
Diploneis crabro	0.1		90/29	TS: 5-6
Diploneis cf. *smithii*	0.1		35/17	TS: 9
Raphid Diatoms (continued)				
Diploneis weissflogii	0.1		25-36/11-15	TS: 9-10
Entomoneis alata	1.6		53-67/15	TS: 16
Frustulia interposita	0.1		117/22	LS: 15; TS: 18
Frustulia vulgaris var. *elliptica*	0.1		42/8.5	TS: ~30
Giffenia cocconeiformis	4.3		37-47/20-23	TS: ~7
Gomphonema biceps	0.1		28/7.5	TS: 12
Gyrosigma diminutum	0.4		100/13	LS: 24; TS: 20
Gyrosigma fasciola var. *globifera*	0.2		77-97/10-12	LS/TS: 24 (equal in number)
Gyrosigma gibbyi	0.3		105/10	LS: 24; TS: 22
Gyrosigma cf. *marcum*	0.1		116/10	LS: 27-30; TS: 28
Gyrosigma cf. *sterrenburgii*	0.5		190-335/22-23	LS: 14; TS: 12
Gyrosigma wansbeckii	5.8		80-101/12-14	LS/TS: 18 (equal in number)
Gyrosigma sp.	2.6		70-74/9-9.5	LS/TS: 24 (equal in number)
Haslea sp.	0.1		35-41/13-14	LS: 24; TS: 13
Navicula acutirostris	0.1		23/6	TS: 18
Navicula flantanica	6.8		41-61/9-12	A: ~20; TS: 9-10
Navicula mannii	0.8		18.5-21/7.5-8.5	TS: 9-10
Navicula pavillardii	0.6		48/9-12	A: ~30; TS: 12
Navicula sp. 1	12.6		34-51/7.5	TS: 11
Navicula sp. 2	2.3		28-38/6-6.5	TS: 12-13
Neidium affine	0.1		46/11	TS: 22
Nitzschia amphibia	0.1		21/4	F: 7; TS: 18
Nitzschia gyrosigma	0.2		300-530/9-9.5	F: 5-6; LS: 21; TS: 24
Nitzschia ligowskii	0.1		25-28/8	F: 9; TS: 27-30
Nitzschia pellucida	2.2		64-65/15	F: 10-11
Nitzschia sigma	0.3		83-87/6.5-7	F: 8-11; TS: 27
Nitzschia sp.	1.8		32.5-57.5 /6.5-7	F: 10-12; TS: 25-27
Pinnularia cf. *parvulissima*	0.1		59/11	TS: 10

Table 2. (Continued)

Species	Relative abundance (%)	Dimension in mm		Density of microstructures in 10 mm
		Diameter	Length/ Width	Areaolae (A), Costae (C), Fibulae (F), Longitudinal Striae (LS), Marginal Processes (MP), Oblique Striae (OS), Striae (S), Transapical Ribs (TR) and Transapical Striae (TS)
Plagiotropis pusilla	0.1		88-105	TS: 16-18
Pleurosigma diverse-striatum	0.1		48-50/14	OS: 20-21; TS: 18
Pleurosigma normanii	0.1		94.5-159 /16.5-24	LS/TS: 18 in the middle, 21 at the apices (equal in number)
Pleurosigma sterrenbergii	0.1		210-215/42-48	LS/TS: ~13 (equal in number)
Psammodictyon panduriforme var. *continua*	0.1		23/9	F: 15; TS: 21
Psammodictyon roridum	0.1		23/9	F: 12; TS: 27
Rhoicosphenia abbreviata	0.1		50/8	TS: 13
Staurophora salina	0.1		49/8	TS: 16
Surirella recedens	0.1		30-53/18.5-35	C: ~2
Surirella sp.	3.2		28-54.5/17-25	C: ~3; TS: ~18
Trachyneis aspera	0.5		70-76/15-17	TS: 9-10
Trachyneis cf. *formosa*	0.3		90/17	TS: 11-12
Tryblionella adducta	0.7		23-24.5/8	TS: 15
Tryblionella coarctata	0.1		52/13	TS: 10
Tryblionella cf. *debilis*	0.1		39/10	F: 8; TR: 11
Tryblionella granulata	8.8		24.5-34 /11.5-13	F: 6.5; TS: 7
Tryblionella hyalina	1.3		18.5-29/9.5-12	F: 9-10; TS: 8.5-10.5
Tryblionella marginulata	0.1		53/10	F: 11; TS: 24
Tryblionella punctata	0.5		34-46.5/ 16.5-20.5	F: 8; TS: 8
Tryblionella salinarum	0.1		28/11	F: 10; TR: 18

and tychoplanktonic species dominated the benthic diatom assemblages at Nanaura mudflat. Among 90 Nanura diatoms, 30 taxa were centric and 60 were pinnate, with four being araphid and fifty-six raphid. Tychoplanktonic species such as *Paralia sulcata*, *Cylotella striata*, and *C. litoralis* dominated centric diatoms, whereas true planktonic ones, such as *Thalassiosira* species, were rare.

Meanwhile, typical brackish (*Aulacoseira granulata*, *Nitzschia sigma*, *Rhoicosphenia abbreviata*, and *Thalassiosira bramaputrae*) and fresh species (*Cycotella stelligera*, *Cymbella turgidula*, *Frustulia vulgaris* var. *elliptica*, *Gomphonema biceps*, *Neidium affine*, and *Nitzschia amphibia*) were also found, collectively accounting for <3% of the diatom assemblages at Nanaura mudflat. The freshwater discharge from the nearby Kase River may have brought and redeposited the six freshwater diatom species into the Nanaura mudflat, especially since only one valve was found and one photo taken for each of them.

Dominant species showing >5% relative abundance were *Navicula* sp. 1 (12.6%) followed by *Paralia sulcata* (10.3%), *Tryblionella granulata* (8.8%), *Navicula flantanica* (6.8%), *Gyrosigma wansbeckii* (5.8%), and *Cyclotella striata* (5.6%). The six species, all of them marine, accounted for about half of the entire diatom assemblages.

Co-occurrence of Nanaura diatoms in Northeast Asia

We selected and compared data from 13 different studies, on 11 benthic habitats (Figure 1), with our results (Table 3). Five out of the six studies on marine benthic

Table 3. List of 77 diatom taxa clearly identified in Nanaura mudflat and their co-occurrence among 11 other benthic habitats from Northeast Asia, based on literature survey of 13 floristic reports of benthic diatoms (see Table 1). Environments of 12 areas (Nanaura plus 11 other habitats) were categorized, according to the salinity information provided by authors, into three groups viz. Marine, Brackish water, and Freshwater. Diatom taxa were listed in three groups (Group I; rarely reported taxa, Group II; mudflat taxa, Group III; brackish & fresh taxa) as the result of cluster anaylsis (+ indicates occurrence of corresponding taxa in a given area).

Group	Diatom taxa	Marine				Brackish				Fresh			
		A[a](J[b])	B(K)	C(C)	D(J)	E(J)	F(J)	G(J)	H(K)	I(K)	J(J)	K(J)	L(J)
Group I	*Amphora richardiana*	+			+								
	Asteromphalus flabellatus	+											
	Cyclotella choctawhatcheeana	+			+								
	Diploneis aestruarii	+			+								
	Ditylum brightwellii	+											
	Eucampia zodiacus	+											
	Gyrosigma diminutum	+											
	Gyrosigma wansbeckii	+											
	Navicula acutirostris	+											
	Navicula flantanica	+			+								
	Navicula pavillardii	+											
	Neodelphineis pelagica	+											
	Nitzschia gyrosigma	+			+								
	Nitzschia ligowskii	+											
	Plagiotropis pusilla	+											
	Psammodictyon roridum	+											
	Rhizosolenia imbricata	+											
	Skeletonema grethae	+											
	Thalassiosira allenii	+											
	Thalassiosira ferelineata	+											
	Thalassiosira lundiana	+											
	Thalassiosira oestrupii var. *ventrickae*	+			+								
	Thalassiosira pacifica	+			+								
	Thalassiosira tenera	+			+								
	Tryblionella adducta	+			+				+				
Group II	*Achnanthes longipes*	+		+		+		+					
	Achnanthes sancti-paulii	+		+				+					
	Actinocyclus octonarius	+		+									
	Actinocyclus octonarius var. *tenellus*	+	+	+			+						
	Actinoptychus senarius	+	+	+	+	+		+					
	Coscinodiscus oculus-iridis	+		+		+							
	Coscinodiscus radiatus	+	+	+		+							
	Cyclotella litoralis	+	+	+	+	+							
	Cyclotella radiosa	+		+									
	Cyclotella striata	+	+	+									
	Cymatotheca weissflogii	+	+	+	+								
	Delphineis surirella	+	+	+	+	+	+						
	Diploneis crabro	+		+									
	Diploneis weissflogii	+	+	+		+							
	Entomoneis alata	+	+	+	+	+							
	Frustulia interposita	+	+	+			+						
	Giffenia cocconeiformis	+	+	+	+	+							
	Gyrosigma fasciola var. *globifera*	+	+										
	Gyrosigma gibbyi	+	+										
	Navicula mannii	+	+		+		+						
	Nitzschia pellucida	+	+			+							
	Paralia sulcata (sensu lato)	+	+	+	+		+	+					
	Pleurosigma diverse-striatum	+	+	+			+						
	Pleurosigma normanii	+	+	+									

Table 3. (Continued)

Group	Diatom taxa	Marine				Brackish				Fresh			
		A[a](J[b])	B(K)	C(C)	D(J)	E(J)	F(J)	G(J)	H(K)	I(K)	J(J)	K(J)	L(J)
	Pleurosigma sterrenbergii	+	+		+								
	Psammodictyon panduriforme var. *continua*	+	+				+						
	Rhaphoneis rhomboides	+	+				+		+				
	Staurophora salina	+	+		+								
	Surirella recedens	+	+	+			+						
	Thalassionema nitzschioides	+	+		+		+						
	Thalassiosira eccentrica	+	+	+		+							
	Thalassiosira nordenskioeldii	+				+							
	Thalassiosira punctigera	+	+										
	Thalassiosira subeccentrica	+		+									
	Trachyneis aspera	+	+	+				+					
	Tryblionella coarctata	+		+		+		+					
	Tryblionella granulata	+	+	+	+	+			+				
	Tryblionella hyalina	+	+	+	+								
	Tryblionella marginulata	+	+										
	Tryblionella punctata	+	+	+	+				+				
	Tryblionella salinarum	+				+						+	
	Tryblioptychus cocconeiformis	+	+	+		+	+						
Group III-1	*Aulacoseira granulata*	+				+	+	+	+	+			+
	Nitzschia sigma	+		+	+	+		+	+				
	Rhoicosphenia abbreviata	+		+	+	+		+	+	+	+		+
	Thalassiosira bramaputrae	+			+	+		+	+				+
Group III-2	*Cyclotella stelligera*	+	+				+			+	+		
	Cymbella turgidula	+	+				+			+	+	+	+
	Frustulia vulgaris var. *elliptica*	+								+		+	
	Gomphonema biceps	+					+				+	+	
	Neidium affine	+					+			+			
	Nitzschia amphibia	+						+		+	+	+	+
No. of occurred taxa		90	34	31	26	20	16	11	8	7	5	5	5

[a]A: Nanaura mudflat (this study), B: Gyeonggi Bay (Choi, 1988; Noh et al., 2001), C: Fujian coast (Jin et al., 1985; Jin et al., 1991), D: Isahaya Bay (Ohtsuka, 2005), E: Matsukawaura Lagoon (Nigorikawa and Hasegawa, 1999), F: Kase River Estuary (Yamakawa, 1994), G: Lake Kamo (Hasegawa and Nigorikawa, 1993), H: Nakdong River Estuary (Cho, 1988), I: Yungchun Dam Reservoir (Lee et al., 1992), J: Ina-gawa River (Houki, 1986), K: Hii River (Ohtsuka, 2002), L: Lake Biwa (Watanabe and Houki, 1988).
[b]A country code to which a given area belongs was given in parenthesis, viz. (C): China, (J): Japan, and (K): Korea.

diatoms were selected, while four of the 13 brackish and four of 15 the freshwater studies were found suitable for comparison purposes. Co-occurrences of Nanaura diatoms across Northeast Asia were provided in salinity groups (viz. in the order of marine, brackish, and fresh) and further arranged according to the number of concurrently occurred species in each group.

As for co-occurrence between Nanaura and other benthic habitats, as expected, relatively larger numbers of species co-occurred as the corresponding salinity increased (viz. <8 in fresh, between 8-20 in brackish, and ≥21 in marine habits, respectively), Interestingly, the greatest number of co-occurred species were not found in Japan, where selected sites, such as Isahaya mudflat (n=26) and Kase River Estuary (n=16), are geographically close to Nanaura mudflat, but in Songdo mudflat, Korea (n=34) followed by the Fujian coast, China (n=31). All together, physical environment (viz. salinity) seemed to prevail over geographical distance (viz. locality) when determining occurrence similarity (or species composition). Meanwhile, certain species found in Nanaura mudflat also co-occurred in freshwater habitats across Japan and Korea (Table 3), but since this was most often a single specimen among all of the corresponding species (n=10), they should not be considered typical mudflat diatoms.

Floral characteristics of Nanaura diatoms

To further find out the floral characteristics in Nanaura mudflat, 77 Nanaura species identified to the species were cluster-analyzed in terms of co-occurrence in Northeast Asia (Figure 2). Cluster analysis clearly exhibited three groups, described below in greater detail.

Group I (n=25) included ‘rarely reported taxa’ throughout the benthic habitats of Northeast Asia. The group included some planktonic species such as *Cyclotella choctawhatceeana*, *Ditylum brightwellii*, *Eucampia zodiacus*,

Table 4. List of taxa which have been alternatively identified in the present study based on authoritative literatures.

Species in question, reported in surveyed literatures (see Table 1)	Description of the species from surveyed literatures			Ddescription of the species given in the authoritative publications[b] (Contradictory to the description of the species to the left)				Suggested identification for the species in question
	Size (μm)	Microstructures in 10 Mm	Additional observation during literature survey in this study[a]	Authoritative publications	Size (μm)	Microstructures in 10 μm	Original morphological information	
Cyclotella striata (Nigorikawa and Hasegawa, 1999)	D: ~14	Striae ~14	Marginal chamber not observed	Lange and Syversten, 1989, p. 348	D: 25-48	Striae 7-13	Marginal chambers (3-4 in 10 μm) present	*Cyclotella litoralis* Lange & Syversten, 1989
Cyclotella stylorum (Nigorikawa and Hasegawa, 2000)	D: ~18	Striae ~14	Marginal chamber not observed	Lange and Syversten, 1989, p. 346	D: 35-67	Striae 9-12	Marginal chambers (2-3 in 10 μm) present	
Coscinodiscus temperei (Jin et al., 1985)	L: 25 W: 20	Areoale 10	Areolae arranged radially	Schmidt et al., 1874-1959, pl. 163, fig. 9	L: ~76 W: ~55	Areolae ~5	Longer thorn' at the valve margin[c]	*Cymatotheca weissflogii* Hendey, 1958
Diploneis oblongella (Hirose et al., 2000)	L: 12.5 W: 6	Striae 18	Valve slightly constricted in the middle	Krammer and Lange-Bertalot, 1986, p. 287	L: 10-40 W: 6-10	Striae 18-24	Valve linear, linear-elliptic to elliptic	*Diploneis aestuarii* Hustedt, 1939
Gomphonema helveticum (Houki, 1986)	L: 27 W: 6	Striae 13	Valve ends capitate, raphe sinuous	Hustedt, 1930, p. 373, fig. 712.	L: 22-60 W: 5-9.5	Striae 12-18	Raphe slightly eccentric, striae weakly radiate	*Gomphonema biceps* Meister, 1935
Gyrosigma balticum (Noh et al., 2001)	L: 290 W: 26	Striae 11-12	Raphe on the central line, or sub-eccentric	Reid and Williams, 2003, p. 137	L: 210-430 W: 25-35	Striae 10-15	Raphe central, undulating	*Gyrosigma* cf. *sterrenburgii* Stidolph, 1992
Navicula platyventris (Yamakawa, 1994)	17-22 6-7	Striae 9-10	Striae parallel at the apices	Meister, 1935, p. 95, fig. 33	10.5-13 5-6.5	Striae 12-15	Valve elliptic with rostrate apices, striae radiate	*Navicula mannii* Hagelstein, 1938
Pleurosigma angulatum (Noh et al., 2001)	L: 183 W: 34	Striae 13	Raphe angle 11°, oblique striae crossed at an angle of 65°	Hendey, 1964, p. 246, pl. 35, figs. 1-3	L: 128-280 W: 36-62	Striae 18-22	Oblique striae set an angle of ~60°	*Pleurosigma sterrenburgii* Stidolph, 1993
Rhaphoneis amphiceros (Choi, 1988)	L: 20-45 W: 10-20	Striae 11	Valve rhombic, sternum very narrow and linear	Hustedt, 1959, p. 174, fig. 680	L: 20-100 W: 18-25	Striae 6-7	Valve lanceolate or rhombic-lanceolate with produced acute apices	*Rhaphoneis rhomboides* Hendey, 1958
Achnanthes manifera (Yamakawa, 1994)	L: 26 W: 12	Striae 10	Valve rhombic, sternum very narrow and linear	Hustedt, 1955, p. 18, pl. 6, figs. 1-8	L: 20-65 W: 7-24	Rv: costae 18-30	RV with transapically dilated fascia	
Surirella fastuosa var. *cuneata* (Hirose et al., 2004)	L: 32 W: 21	Costae 2	Short costae on the cuneate side of the valve	Schmidt et al., 1874-1959, pl. 4, figs. 1,2	L: 112-132 W: 64-76	Costae ~1.5	Valve ovate[b]	*Surirella recedens* Schmidt, 1875
Surirella fluminensis (Noh et al., 2001)	L: 43 W: 30	Costae 2	Short costae on the cuneate side of the valve	Schmidt et al., 1874-1959, pl. 5, fig. 6	L: 59 W: 28	Costae ~1.5	Valve ovate[b]	
Trachyneis antilarum (Noh et al., 2001)	L: 65 W: 17	Striae 11	Axial area linear & unilateral, central area elliptic	Cleve, 1894, p. 193	L: 120-170 W: 26-32	Striae 9-10	Axial area naviculoid, raphe eccentric	*Trachyneis* cf. *formosa* Meister, 1932
Trachyneis clepsydra (Jin et al., 1985)	L: 67-82 W: 17	Striae 10-11	Axial area linear & unilateral, central area elliptic	Cleve, 1894, p. 192	L: 110-130 W: 20	Striae 10	Indistinctive axial area, raphe central	
Nitzschia navicularis (Jin et al., 1985)	L: 35-47 W: 14-18	Striae 7	Stirae uniseriate	Krammer and Lange-Bertalot, 1988, p. 45	L: 30-80 W: 15-25	Striae 6-8	Striae biseriate, fibulae 6-8 in 10 mm	*Tryblionella hyalina* (Amossé) Ohtsuka, 2005
Nitzschia navicularis (Choi, 1988)	L: 40 W: 18	Striae 7	Striae uniseriate					

[a]Species descriptions were poor and/or not given in the literatures, thus mesurement and/or description of the speceis are made based on photographsic information.
[b]Original literatures, taxonomical review papers and so on.
[c]Originally written as "An der Seite pflegt ein laengerer Dorn vorzustehen, welcher an dem gezeichneten Exemplar abgebrochen war"

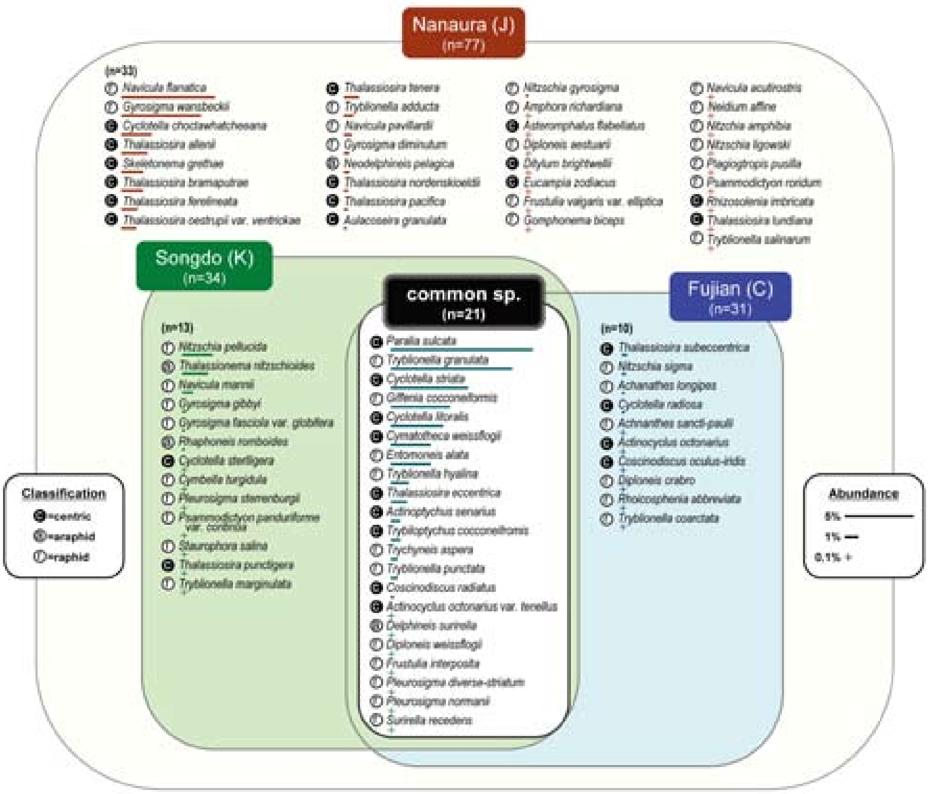

Figure 3. Co-occurrence of Nanaura diatoms in Songdo mudflat (Korea) and Fujian coast (China). Relative abundance (%) and diatom classification (centric, araphid, and raphid) are also provided.

Rhizosolenia imbricata, and *Thalassiosira* spp., not considered typical benthic taxa. Included in our material was the planktonic *Skeletonema grethae,* recently described as "new to science" (Sarno et al., 2005). *Nitzschia gyrosigma*, which is similar to *N. sigmoidea*, was also newly described from Northeast Asia (Ohtsuka, 2005).

Group II (n=42) consisted of mostly marine and brackish-marine taxa, thus designated 'coastal and mudflat taxa'. Many of them occurred concurrently not only in marine environments such as Songdo mudflat, Korea and Fujian coast, China, but also in brackish water environments e.g., Matsukawaura Lagoon, Japan (Nigorikawa and Hasegawa, 1999). Most of the centric diatoms in the group, i.e., *Coscinodiscus* spp., *Cyclotella* spp., *Paralia sulcata*, and *Thalassiosira eccentrica* are often found in coastal sediments and are thought to be neritic species (Witkowski et al., 2000). Pennate diatoms in the group (e.g., *Diploneis* spp., *Gyrosigma* spp., *Pleurosigma* spp., and *Tryblonella* spp. etc.) are mostly mudflat taxa.

Group III (n=10) was rather small in number but could be further divided into two sub-groups. Group III-1 consisted of 4 species of *Aulacoseira granulata*, *Nitzschia sigma*, *Rhoicosphenia abbreviata*, and *Thalssiosira bramaputrae*. They were found throughout Northeast Asia across a wide range of salinities but particularly in brackish environments. Group III-2 consisted of typical freshwater species *Cycotella stelligera*, *Cymbella turgidula*, *Frustulia vulgaris* var. *elliptica*, *Gomphonema biceps*, *Neidium affine*, and *Nitzschia amphibia*. Altogether, Group III was designated 'brackish and freshwater taxa'.

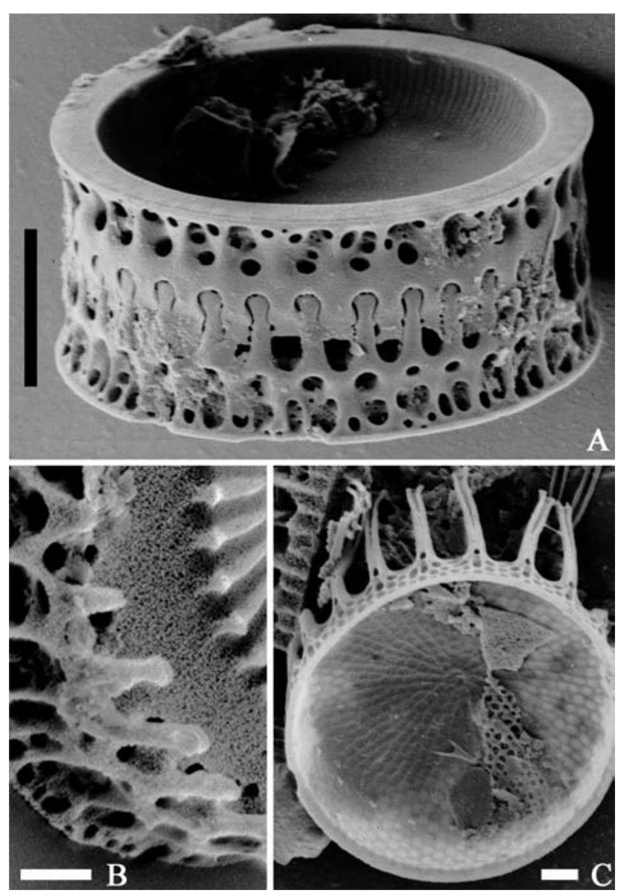

Figure 4. SEM photos of *Paralia sulcata* (A, B) and *Skeletonema grethae* (C). Scale bar = 1 μm in A, B, 5 μm in C.

DISCUSSION

Regional distribution of the Nanaura diatoms in Northeast Asia

As for Japanese marine habitats, the diatom flora of Isahaya Bay in the western Ariake Sea was found most comparable to that of Nanarua mudflat, with 26 taxa in common. The number seems rather low considering 1) their relative closeness within the Ariake ecosystem (ca. 50 km apart) and 2) their similar substratum of fine mud. The dominant Isahaya mudflat species apparently differed from those found in Nanaura mudflat; *Haslea nipkowii* was the most dominant (ca. 20% abundance) followed by *Paralia sulcata* (ca. 11%), *Cyclotella litoralis* (ca. 9%), and *Nitzschia gyrosigma* (ca. 8%) in Isahaya Bay (Ohtsuka, 2005). One possible cause would be the influence of freshwater

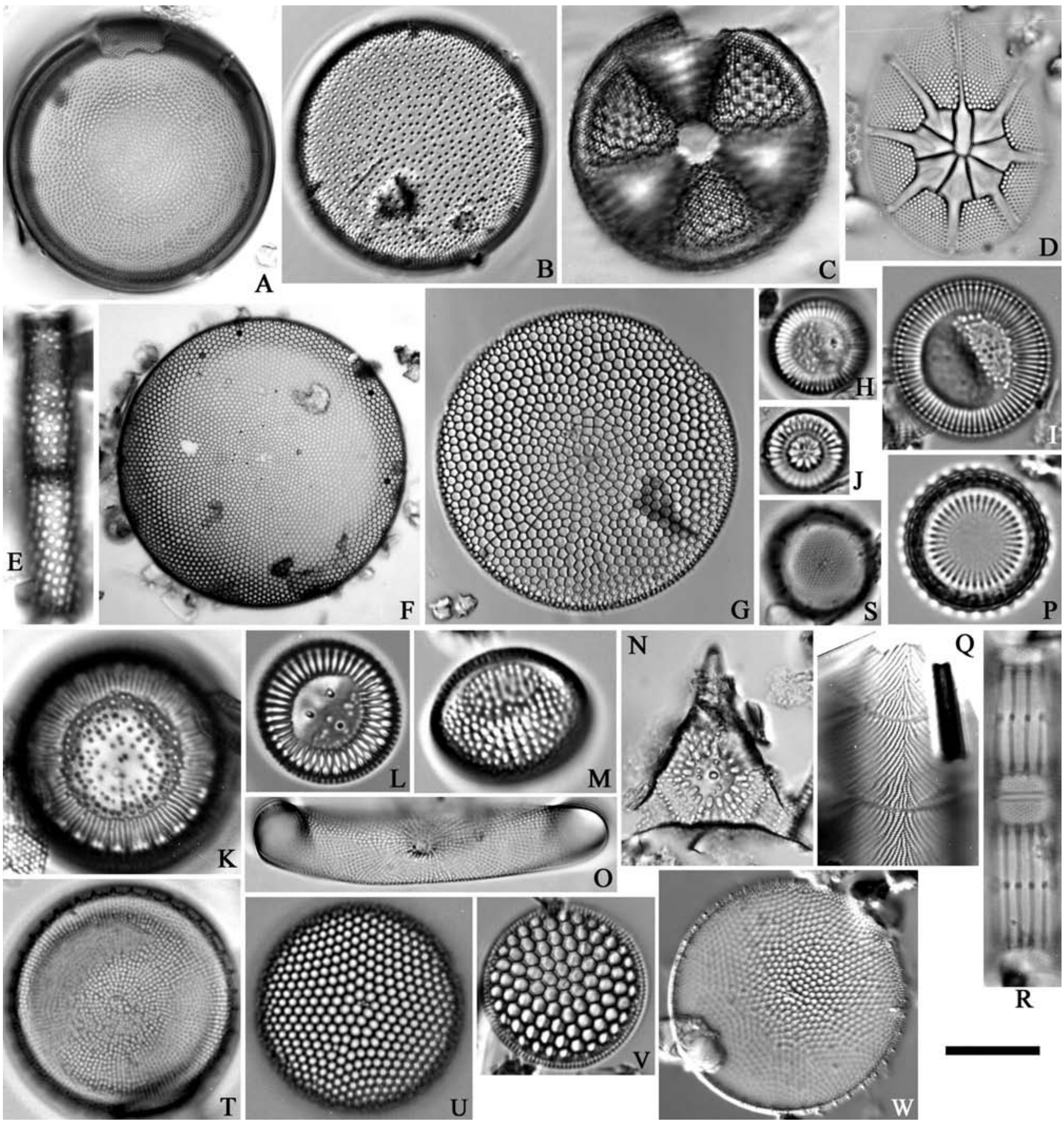

Figure 5. LM photos of Nanaura diatoms. A, *Actinocyclus octonarius*; B, *A. octonarius* var. *tenellus*; C, *Actinoptychus senarius*; D, *Asteromphalus flabellatus*; E, *Aulacoseira granulata*; F, *Coscinodiscus oculus-iridis*; G, *C. radiatus*; H, *Cyclotella choctawhatcheeana*; I, *C. litoralis*; J, *C. radiosa*; K, *C. stelligera*; L, *C. striata*; M, *Cymatotheca weissflogii*; N, *Ditylum brightwellii*; O, *Eucampia zodiacus*; P, *Paralia sulcata*; Q, *Rhizosolenia imbricate*; R, *Skeletonema grethae*; S, *Thalassiosira allenii*; T, *T. bramaputrae*; U, *T. eccentric*; V, *T. eccentrica* var. *fasciculata*; W, *T. ferelineata*. Scale bar = 10 μm in C-E, H-N, P, R-W, 15 μm in A, B, F, G, O, Q.

discharge from several rivers including the Kase River on the Nanaura assemblages, which is supported by the fact that none of the freshwater species (viz. Group III-2) were reported in the Isahaya Bay (Table 3). Although 'Honmyo River' flows into Isahaya Bay, it may not be comparable to the Kase River, due to its small scale. Seasonality could be another reason for the different species composition, considering the different sampling time in Isahaya (May) and Nanaura (October). Among brackish water habitats in Japan, the diatom flora in Matsukawaura Lagoon was the most similar to that of Nanaura mudflat, showing 20 species in common. The rather high number of concurrently occurred species found in Matsukawaura Lagoon could be attributed to the comparably high salinity (ca. 30‰).

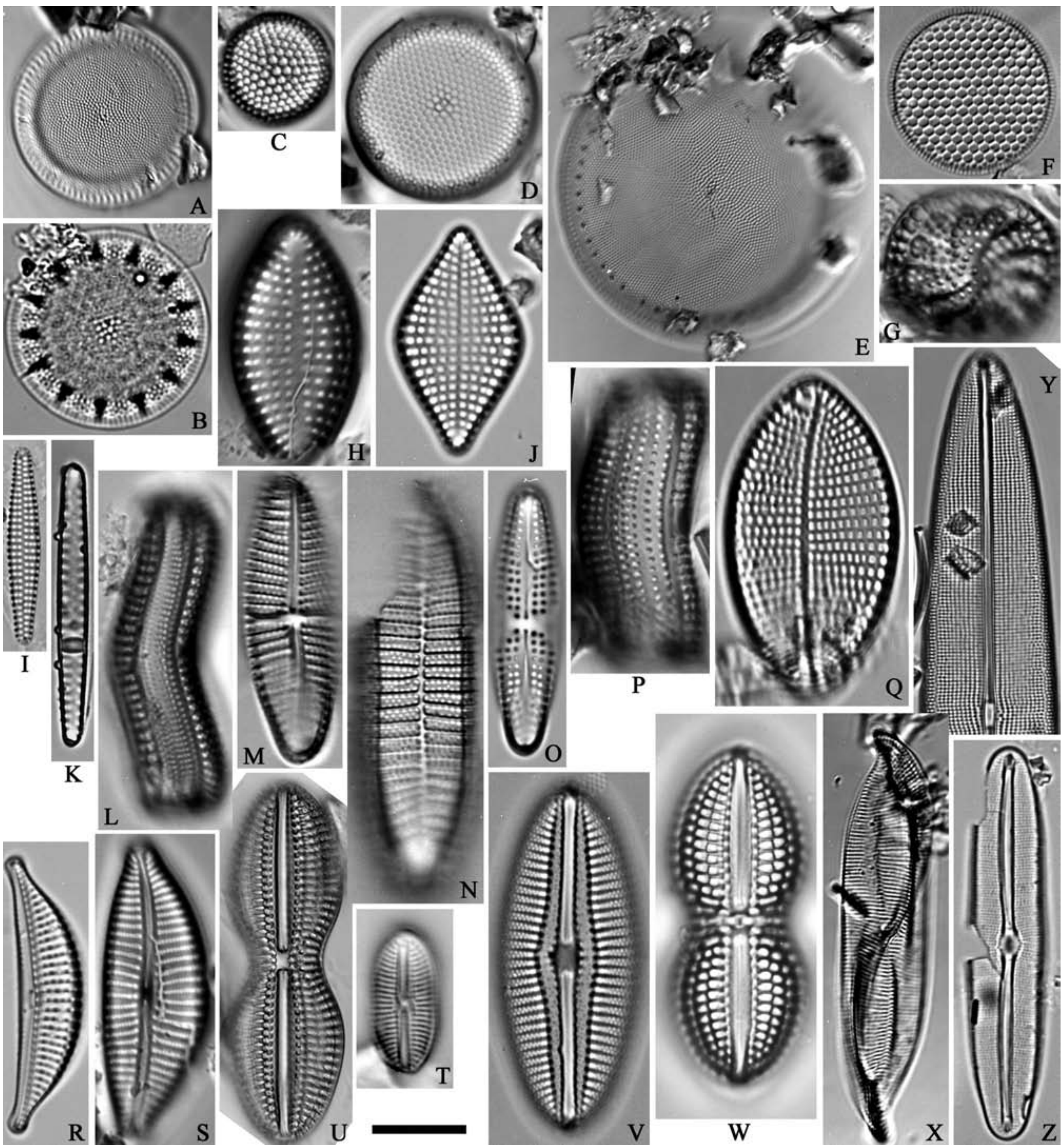

Figure 6. LM photos of Nanaura diatoms. A, *Thalassiosira lundiana*; B, *T. nordenskioeldii*; C, *T. oestrupii* var. *venrickae*; D, *T. pacifica*; E, *T. punctigera*; F, *T. tenera*; G, *Tryblioptychus cocconeiformis*; H, *Delphineis surirella*; I, *Neodelphineis pelagic*; J, *Rhaphoneis rhomboids*; K, *Thalassionema nitzschioides*; L, M, N, *Achnanthes longipes*; O, P, *A.* cf. *pseudogroenlandica*; Q, *A. sancti-paulii*; R, *Amphora richardiana*; S, *Cymbella turgidula*; T, *Diploneis aestuarii*; U, *D. crabro*; V, *D.* cf. *smithii*; W, *D. weissflogii*; X, *Entomoneis alata*; Y, *Frustulia interposita*; Z, *F. vulgaris* var. *elliptica*. Scale bar = 10 μm in A-D, F, G, H-T, V, W, Z, 15 μm in E, U, X, Y.

Meanwhile, only a few species (n = 10), mostly of Group III, were reported from benthic habitats in freshwater environments.

Nanaura diatoms also concurrently occurred in Songdo mudflat, Korea (n = 34) and Fujian coast, China (n = 31) (Figure 3). Twenty one species, namely *Actinocyclus octonarius* var. *tenellus*, *Actinoptychus senarius*, *Coscinodiscus radiatus*, *Cyclotella litoralis*, *C. striata*, *Cymatotheca weissflogii*, *Delphineis surirella*, *Diploneis weissflogii*, *Entomoneis alata*, *Frustulia interposita*, *Giffenia cocconeiformis*, *Paralia sulcata*, *Pleurosigma diverse-striatum*, *P. normanii*, *Surirella recedens*, *Thalassiosira eccentrica*,

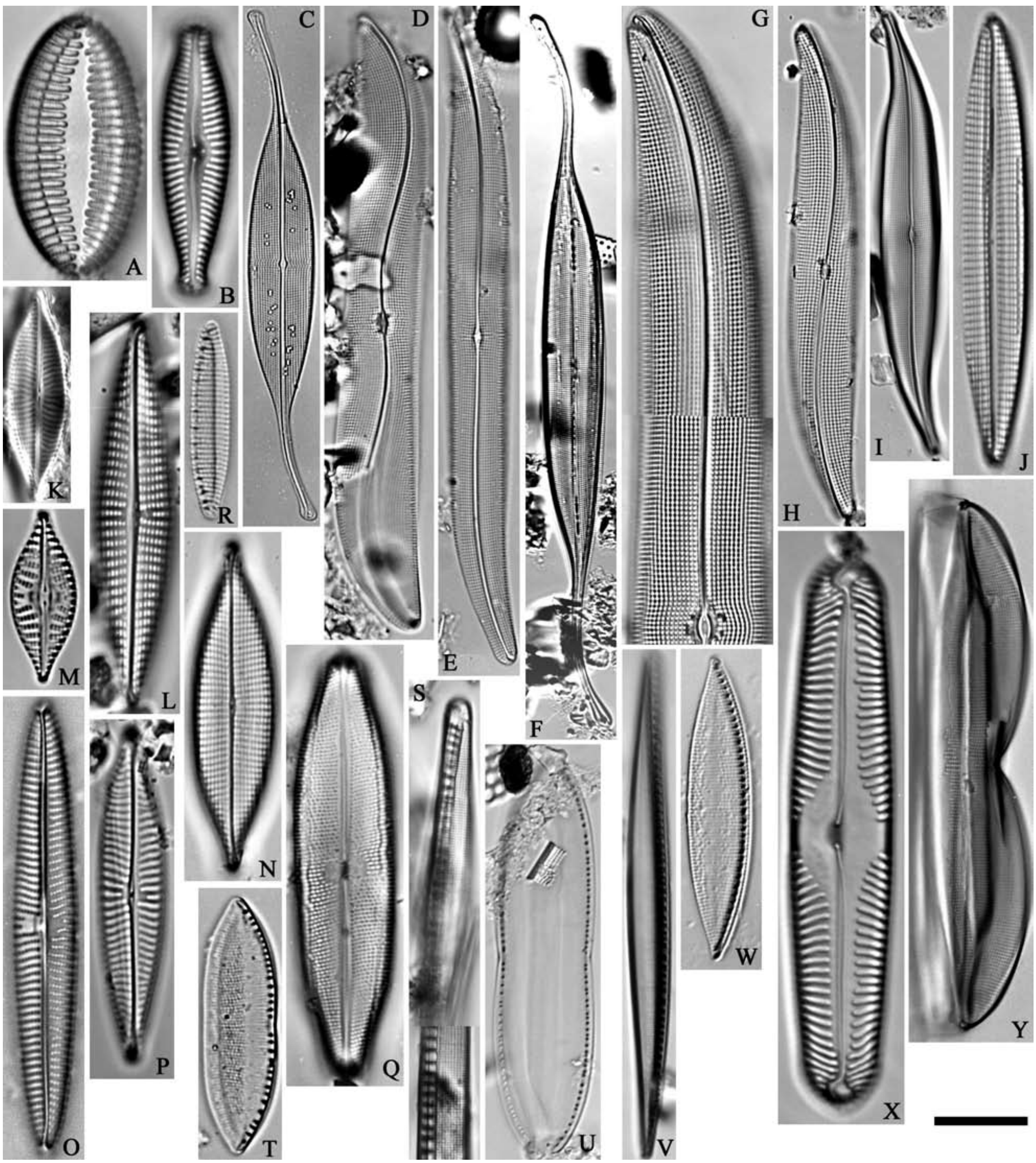

Figure 7. LM photos of Nanaura diatoms. A, *Giffenia cocconeiformis*; B, *Gomphonema biceps*; C, *Gyrosigma faciola* var. *globifera*; D, *G. diminutum*; E, *G. gibbyi*; F, *G.* cf. *macrum*; G, *G.* cf. *sterrenburgii*; H, *G. wansbeckii*; I, *G.* sp.; J, *Haslea* sp.; K, *Navicula acutirostris*; L, *N. flantanica*; M, *N. mannii*; N, *N. pavillardii*; O, *N.* sp. 1.; P, *N.* sp. 2.; Q, *Neidium affine*; R, *Nitzschia amphibia*; S, *N. gyrosigma*; T, *N. ligowskii*; U, *N. pellucida*; V, *N. sigma*; W, *N.* sp.; X, *Pinnularia* cf. *parvulissima*; Y, *Plagiotropis pusilla*. Scale bar = 10 µm in A, B, J-R, T. W-Y, 15 µm in C-I, S, U, V.

Trachyneis aspera, *Tryblionella granulata*, *T. hyalina*, *T. punctata*, and *Trybiloptychus cocconeifromis* were common across Nanaura, Songdo, and Fujian, representing typical diatom taxa for Northeast Asia and accounting for 43.3% of the total. Among the above species, the dominant species (>5%) are *Paralia sulcata* (10.3%), *Tryblionella granulata* (8.8%), and *Cyclotella striata* (5.6%), collectively accounting for ca. 60% of total common species.

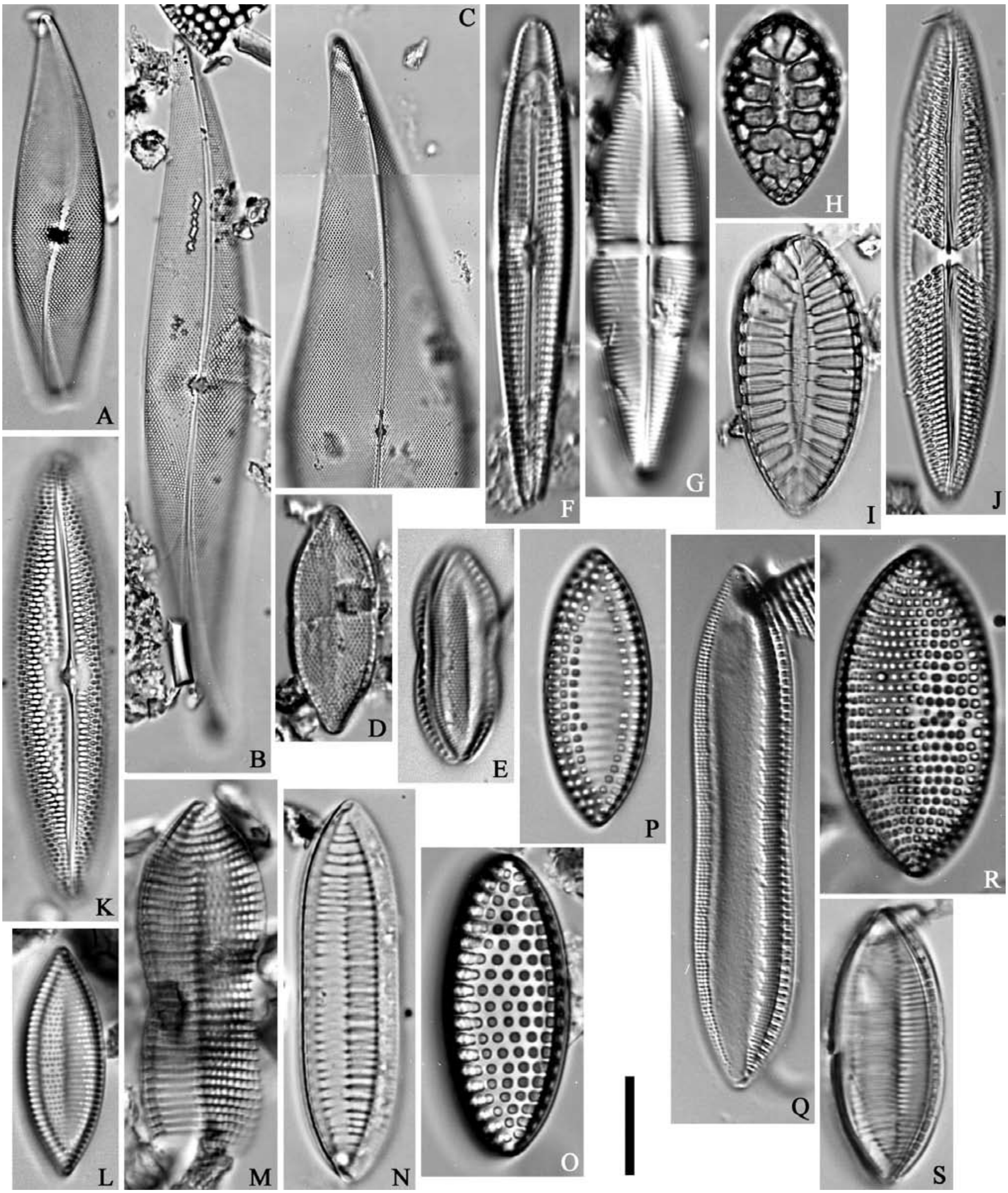

Figure 8. LM photos of Nanaura diatoms. A, *Pleurosigma diverse-striatum*; B, *P. normanii*; C, *P. sterrenburgii*; D, *Psammodictyon panduriforme* var. *continua*; E., *P. roridum*; F, *Rhoicosphenia abbreviata*; G, *Staurophora salina*; H, *Surirella recedens*; I, *S.* sp.; J, *Trachyneis aspera*; K, *T.* cf. *formosa*; L, *Tryblinonella adducta*; M, *T. coarctata*; N, *T.* cf. *debilis*; O, *T. granulata*; P, *T. hyalina*; Q, *T. marginulata*; R, *T. punctata*; S, *T. salinarum*. Scale bar = 10 μm in D, E-G, L-S, 15 μm in A, B, H-K, and 20 μm in C.

Overall, the above species comprised a relatively great proportion of Nanaura mudflat both individually and collectively and are thus likely abundant and widespread across Northeast Asia.

Worldwide occurrence of Nanaura diatoms

Certain species among the Nanaura assemblages were distributing worldwide. Species such as *Actinocyclus octonarius*, *Actinoptychus senarius*, *Coscinodiscus oculus-iridis*, *Entomoneis alata*, *Nitzschia pellucida*, *Paralia sulcata*, *Pleurosigma normanii*, *Thalassionema nitzschioides*, *Thalassiosira eccentrica*, *Tryblionella granulata*, and *T. salinarum* have been reported as cosmopolitan species in the coastal areas (Hasle and Syvertsen, 1997; Witkowski et al., 2000). Previous reports of *P. sulcata*, however, may be of one of three *Paralia* spp., viz. *P. capitata*, *P. fenestrata*, and *P. sulcata* (Sawai et al., 2005), thus further study is needed to verify the worldwide distribution of *P. sulacata,* sensu stricto. *Nitzschia ligowskii*, recently described as new to science, has also been reported as distributing worldwide (Witkowski et al., 2004).

A few diatoms that appeared among Nanaura assemblages have rarely been reported worldwide. *Gyrosigma gibbyi* was first described in New Zealand in 2003 and our study is the second report of this species in the world and the first in the northern hemisphere. *Gyrosigma gibbyi* was also recorded in the Korean mudflat as *Gyrosigma* sp. (Noh et al., 2001) thus possibly widespread in Northeast Asia. *Nitzschia gyrosigma*, first described in Isahaya Bay (Ohtsuka, 2005), was also observed in the present study. So far the locality of *N. gyrosigma* is limited to the Ariake Sea, Japan, however, the corresponding species was observed in the Korean mudflat (personal observation). Thus it is possible that *N. gyrosigma* is widespread across Northeast Asia yet reported as *N. sigmoidea,* which is very similar (Ohtsuka, 2005) under LM observation. The first report of three for *Pleurosigma sterrenburgii* is from New Zealand (Stidolph, 1993) followed by two more from the German Wadden Sea (Sterrenburg, 2003; 2005). Thus our study is the first report of the species in Asia, second in the Northern Hemisphere, and fourth worldwide. *Pleurosigma sterrenburgii* was also recorded in the Korean mudflat as *P. angulatum* (Noh et al., 2001) supporting the possible endemism of the taxon in the marine littoral as suggested by Sterrenburg (2003). *Skeletonema grethae*, first described in 2005, is another species with few reports worldwide. Kooistra et al. (2008) stated that "it is clear that most *Skeletonema* species are widely distributed throughout either temperate or tropical coastal regions" and "*S. grethae* is apparently the only exception to the widespread distribution of the species with its distribution only along the Atlantic side of the USA". However, provided that our identification is correct, the distribution of *S. grethae* should be greater, and include the Pacific Ocean. There was also a record of *S. grethae* from the Pacific coast of Canada (Sarno et al., 2005), which was somehow not counted by Kooistra et al. (2008). Thus, distribution of *S. grethae* may not be restricted to Atlantic Ocean.

Furthermore, there seemed to be some rarely reported species in the Western Hemisphere and Europe that are common in Northeast Asia. *Cymatotheca weissflogii*, which was first described on the western coast of Africa (Hendey, 1958), has not seemingly been reported from USA and Europe. The only record of its location in the Western Hemisphere is in Brazil (Priscila et al., 2008), with a couple of reports of it in Northeast Asia (Jin et al., 1985; Choi, 1988; Ohtsuka, 2005). Rarely reported from the Western Hemisphere is also *Tryblioptychus cocconeiformis,* which was first reported in 1883 by Cleve from Labuan near Borneo (Prasad et al., 2002). Its distributions are somehow global, however, there are only two records from the Western Hemisphere, viz. one from Florida, USA (North America) and the other from Georgetown, Guyana (South America), with no record from Europe. On the contrary, there were many reports of the taxon from the East Asia (Prasad et al., 2002). All together, *C. weissflogii* and *T. cocconeiformis*, which co-occurred among the mudflats of Japan, Korea and China (Figure 3), are considered characteristic of the Northeast Asian mudflats. Overall, the benthic diatom species found in Nanaura mudflat showed a wide spectrum of biogeographical distribution; some were cosmopolitan, some were typical of the mudflats of Northeast Asia, and some were rare worldwide (Figure 3).

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日本明海七浦灘塗的硅藻：遠東地區硅藻的分類與區域分布

朴鎮淳[1] 金宗聲[1] 大塚泰介[2] 荒木宏之[3] Andrzej WITKOWSKI[4] 高哲煥[5]

[1] 韓國高麗大學 環境生態工學部

[2] 日本琵琶湖博物館

[3] 日本佐賀大學 低地和海洋研究所

[4] 波蘭什切青大學 海洋科学研究所古海洋部

[5] 韓國國立首爾大學 地球環境科學部

本文研究了日本明海沿岸七浦灘塗 (E 130° 10´, N 33° 04´) 底栖硅藻 (Bacillariophyceae) 的植物區系特徵和多樣性。同時開展了文獻檢索以更好地瞭解東北亞地區海洋底棲矽藻的地理分佈。通過光學顯微鏡和掃描電鏡觀察發現七浦矽藻共有 90 種。本文列出了這些矽藻物種的名稱並提供了相應的立體資訊和顯微結構密度，必要時給出了超微結構。優勢種依次爲 *Navicula* sp. 1 (12.6%), *Paralia sulcata* (10.3%), *Tryblionella granulata* (8.8%), *Navicula flantanica* (6.8%), *Gyrosigma wansbeckii* (5.8%) 和 *Cyclotella striata* (5.6%)。這 6 種矽藻大約占了豐度總量的 50%。而按照對鹽度的需求劃分，海水和苦咸水種是優勢種，但也發現了微咸水和淡水種。被研究地點的矽藻植物區系組成與日本灘塗（例如諫早灣）和微咸水潟湖（松川浦）以及韓國的松島灘塗和中國的福建沿海等地的情況比較相似。考慮到矽藻的棲息地和資料品質，我們選擇了來自東北亞的 13 份報告進行比較。結果發現包括 *Cymatotheca weissflogii* 和 *Tryblioptychus cocconeiformis* 在內的 21 種七浦矽藻似乎在日本、韓國和中國都有分佈，而西半球和歐洲的相關報導卻很少，因此這些底棲矽藻被認爲是東北亞地區普遍存在的種。

關鍵詞：生物地理學；硅藻植物區系；日本；灘塗；東北亞。