Miocene to Pleistocene paleogeographic distributions of polycystine radiolarians in the North Pacific

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Abstract

Paleogeographic distributions in the North Pacific and their changes in 58 Miocene–Pleistocene polycystine radiolarians were documented at intervals of 18–19, 15–16, 12–13, 9–10, 3–4, and 1–2 Ma. Their patterns were categorized into eight groups based on their geographic distributions: (1) equatorial – low latitude group, (2) western equatorial to low latitude group, (3) eastern low to mid-latitude group, (4) low to mid-latitude group, (5) middle latitude group, (6) high latitude group, (7) east group, (8) cosmopolitan group and (9) no significant group. Several phylogenetic groups showed different distribution patterns between ancestors and descendants, suggesting immigration and competition. In addition, the applicable area of the known radiolarian biozonation was also evaluated from geographic distributions.

Key words: Miocene, Pliocene, Pleistocene, North Pacific, Radiolaria

Introduction

The geographic distributions of planktonic protistan fossils such as planktonic foraminiferans, nannofossils, radiolarians, and diatoms are highly informative in paleoceanography because the faunal composition of the surface sediments corresponds approximately to the undissolved faunal composition of the living assemblage above the deposition site (e.g., Okada and Honjo, 1973; Takahashi and Honjo, 1981). However, sea floors of the North Pacific are mostly below the carbonate compensation depth (CCD; Berger, 1976) and thus, too deep to preserve calcareous fossils. This is one of the reasons for that siliceous microfossils are important paleoceanographic proxy in the pelagic part of the North Pacific. In particular, polycystine radiolarians, which are unicellular marine planktonic Protista with siliceous skeletons, tend to be preserved preferentially in such carbonate-poor sediments.

Biogeographic studies of Pleistocene to Holocene polycystines in the North Pacific show significant distribution patterns corresponding to the distribution of water masses (Kruglikova, 1969, 1999; Nigrini, 1970; Ling et al., 1971; Ling, 1974; Lombari and Boden, 1985; Nimmergut, 2002; Motoyama and Nishimura, 2005). In contrast, the distributions of Miocene to Pliocene polycystines have only been described (e.g., Sanfilippo et al., 1985) or mapped over limited time intervals for a few species (Lombari, 1985; Romine, 1985). Here, we illustrate the geographic distributions of 58 polycystine taxa in the North Pacific at time intervals of 18–19, 15–16, 12–13, 9–10, 6–7, 3–4, and 1–2 Ma, and discuss about some implications of these spatial distribution patterns.

Material and methods

The samples were selected from the Miocene to Pleistocene polycystine-bearing sediments of Deep Sea Drilling Project (DSDP) and Ocean Drilling Program (ODP) sites in an attempt to cover the entire North Pacific region. The DSDP microscope slides for radiolarian analyses were partly borrowed from the Micropaleontology Reference Center (MRC) of the National Science Museum, Tokyo (Table 1). Supplemental samples from DSDP/ODP Sites 184, 445, 462, 581, 806, 883, 884, and 1207, which are not archived at the MRC, were newly prepared or were borrowed from K. Ogane and E. Yoshimura. The depositional age was estimated by Lazarus et al. (1995) for DSDP samples and by Barron et al. (1995), Chaisson and Leckie (1993), and Takayama (1993) for ODP samples, following the age conversion of Berggren et al. (1995). The locations selected were based on

Site Hole/Core-Section/Interva	age (Ma)	Site Hole/Core-Section/Interva	age (Ma)
71/30-6/29-36	18.4	440B/35-3/20-27	3.2
72/2-5/68-75	6.2	442A/19-CC	6.2
72/3-3/94-101	9.5	442A/24-3/61-68	10.0
72/4-6/53-60	12.6	442A/25-3/58-65	12.0
72/5-1/117-124	15.5	445/35-4/40-41	18.1
173/9-3/24-30	1.8	458/7-3/63-70	9.8
173/19-4/72-78	9.6	458/9-CC	12.6
183/9-4/63-68	1.8	462/3-2/55-62	1.8
183/11-4/58-64	3.3	462/4-2/76-83	3.0
183/15-3/83-88	6.0	462/8-1/77-79	6.8
183/19-2/72-77	9.3	462/10-5/46-48	9.3
184 17-2 20-43	6.9	462/14-5/75-77	12.8
192/5-5/130-135	1.5	468B/6-3/91-98	12.3
192/13-3/59-65	3.9	468B/16-1/27-37	15.9
192/22-1/117-124	6.8	469/5-5/72-80	1.8
289/6-4/72-78	1.8	469/8-3/62-69	3.2
289/13-3/76-82	3.8	472/5-2/126-135	6.8
289/31-4/84-90	9.2	472/7-2/117-125	9.3
289/44-3/64-70	12.6	472/9-1/69-78	12.1
289/56-2/55-61	16.0	493/17-CC	9.2
289/62-1/79-85	18.6	503A/9-2/48-55	1.7
310/4-2/103-109	1.7	503A/20-2/52-59	3.8
310/6-2/83-90	3.2	503A 44-2 108-115	6.8
310/8-4/103-109	7.0	572A/3-6/101-108	1.7
310/9-1/145-150	9.2	572A/6-3/34-41	3.8
315/1-6/130-138	1.0	572D/14-2/134-141	9.8
315/4-6/120-127	4.0	572D/24-1/44-51	12.4
315A/1-5/117-123	6.1	572D/33-1/94-101	15.4
315A/3-5/42-49	9.9	575/1-4/70-77	1.8
315A/4-2/55-62	12.5	575/2-1/43-50	3.2
315A/6-1/67-73	15.9	577/3-4/61-68	1.8
317B/9-2/40-47	6.6	577/5-2/101-109	3.3
317B/13-1/100-106	9.2	578/13-1/20-27	6.0
317B/16-2/31-37	12.3	581/4-6/75-77	6.6
317B/18-6/106-113	15.8	581/7-1/23-25	9.6
317B/20-6/116-123	18.1	586B/18-1/71-78	6.0
433A/6-1/27-34	6.7	806B/23-2/50-51	6.1
438A/39-4/132-139	6.2	883B/49-2/135-137	6.9
438A/58-1/118-125	9.4	883B 63-7 18-20	15.5
438A/65-1/128-135	12.0	883B 66-2 121-123	18.3
438A/73-5/31-38	15.2	884B 50-3 22-23	9.2
440B/16-3/27-34	1.8	884B 58-1 130-131	12.2

Table 1. Sample list

the original position of each site in the past in consideration with plate motion indicated by the reconstruction map of the Ocean Drilling Stratigraphic Network (ODSN) web site (http://ww.odsn.de/; Fig. 1). Maps were made at approximately 1.0 m.y. intervals: 18–19, 15–16, 12–13, 9–10, 6–7, 3–4, and 1–2 Ma. A few cores were recovered in the central North Pacific (Fig. 1), where red clay is widely distributed (Lisitsyin, 1974). Samples with highly dissolved or ill-preserved polycystines were omitted from the data. We examined the slides of radiolarians and plotted the presence and absence of selected

species (Tables 2 and 3). Although quantitative data could provide valid information for understanding paleogeographic distributions, we hesitated to count radiolarian specimens because of the condition of the MRC radiolarian slides. A total of 72 taxa with few taxonomic problems were recorded, and 58 of these were mapped herein. In addition, published papers containing photographs of the selected species were referred on our maps after we checked their identification using current taxonomy. The verified papers will be listed in a website for this journal because the list of more than 100 papers consumes



Fig. 1. Sampling locations after correction for plate motion. Numbers represent Deep Sea Drilling Project (DSDP) and Ocean Drilling Program (ODP) sites.

Distribution map of Miocene–Pleistocene Radiolaria in the North Pacific

Table 2. Li	st of the	selected	radiolar	ian taxa.

Taxon name	Figure number
Amphymenium amphistylium Haeckel	44
Anthocyrtella (?) callopsima Caulet	45
Anthocyrtidium ehrenbergi (Stöhr)	8
Anthocyrtidium jenghisi Streeter	46
Anthocyrtidium ophirensis (Ehrenberg)	58
Anthocyrtidium pliocenica (Seguenza)	47
Artiscins group	10
Artostrobus annulatus (Bailey)	48
Botryostrobus miralestensis (Campbell et Clark)	52
Botryostrobus spp.	29
Calocycletta spp.	2
Carpocanium spp.	9
Cinclopyramis spp.	19
Cornutella profunda Ehrenberg	20
Cycladophora cornuta (Bailey)	40
Cycladophora davisiana Ehrenberg	21
Cycladophora sakaii Motoyama	16
Cyrtocapsella cornuta Haeckel	3
Cyrtocapsella japonica (Nakaseko)	53
Cyrtocapsella tetrapera Haeckel	23
Cyrtolagena pectinata (Haeckel) group	24
Dictyophimus spp.	30
Dorcadospyris alata (Riedel)	36
Dorcadospyris dentata Haeckel	37
Eucyrtidium asanoi Sakai	34
Eucyrtidium spp.	31
Heliodiscus asteriscus Haeckel	11
Lamprocyclas spp.	13
Lamprocyrtis spp.	32
Lithocampe (?) yatsuoense (Nakaseko)	54
Lithocampe chytra Tan	55
Lithopera (Glomeria) baueri Santilippo et Riedel	38
Lithopera (Glomeria) thornburgi Sanfilippo et Riedel	39
Lithopera (Lithopera) bacca Ehrenberg	56
Lithopera (Lithopera) neotera Sanfilippo et Riedel	12
Lithopera (Lithopera) renzae Santilippo et Riedei	17
Lychnocanoma magnacornuta Sakal	1/
Lychnocanoma parallelipes Moloyania	18
Lycnnocanoma spp. (excluding Lycnnocanoma magnacornuta	33
Bhormogurtig algrandrag O'Connor	41
Phormocyrtis diexanarde O Collifor	41 57
Phormostichoartus doliolum (Piedel et Sanfilinno)	57
Phormostichoartus fistula Nigrini	51
Phormostichoartus maniandicus (Martin)	5
Pterocanium audar (Riedel)	35
Pterocanium spn (exclusive of P audar)	14
Pterocorvs spp. (exclusive of 1 : dadax)	15
Saturnalis circularis Haeckel	22
Sinhocampe arachnea (Ehrenberg) group	49
Siphocampe lineata (Ehrenberg) group	50
Siphostichartus corona (Haeckel)	6
Spongurus cylindricus Haeckel	28
Stichocorys armata (Haeckel)	42
Stichocorvs delmontensis (Campbell et Clark)	25
Stichocorvs peregrina (Riedel)	26
Stichocorvs wolffii Haeckel	43
Theocorythium spp.	59
Xiphosphaerantha angelina (Campbell et Clark)	27
,, composition of chain,	

the page space of our paper. On the geographical maps (Figs. 2–59), filled circles indicate the presence of a taxon by our examination, open circles indicate the absence of a taxon by our examination, and solid boxes indicate presence data from previous publications.

Results

The 58 selected polycystine taxa showed highly variable changes in their distribution patterns through time. The

distribution patterns of these taxa can be divided roughly into eight groups: (1) equatorial – low latitude group, (2) western equatorial to low latitude group, (3) eastern low to mid-latitude group, (4) low to mid-latitude group, (5) middle latitude group, (6) high latitude group, (7) east group, (8) cosmopolitan group and (9) no significant group, although many species have changed the distribution limit in the examined time-intervals.

1. Equatorial – low latitude group (Figs. 4, 5)

This group consists of the species that distributed at latitudes lower than 30° N in the North Pacific, comprising *Phormostichoartus doliolum* (Riedel et Sanfilippo) (Fig. 4) and *Phormostichoartus marylandicus* (Martin) (Fig. 5).

The oldest occurrence of *P. doliolum* is Serravallian, recovered at Vityaz's Station 5133 in the low-latitude Pacific (Kruglikova, 1974), although Nigrini (1977) stated that this species appeared from the *Ommatartus antepenultimus* Zone (Late Miocene) and was extinct in the early Pliocene. *P. doliolum* (Fig. 4) was reported by Kruglikova (1974) from the low-latitude western Pacific at 15–16 Ma. We found this species in the western to central equatorial Pacific and the mid-latitude (20°) eastern Pacific at 12–13 Ma. This species occurred from the equatorial Pacific and Site 442, western Pacific, at 9–10 Ma. It was restricted to the low-latitudes at 6–7 and 3–4 Ma. *P. marylandicus* (Fig. 5), which first appeared in the Oligocene,

is the ancestor of *P. doliolum* (Nigrini, 1977). This species was present in the low-latitude Pacific from 18–19 to 9–10 Ma, but the limit of its distribution changed through time. At 15–16 Ma, this species was found around California, but retreated to the equatorial Pacific at 12–13 Ma and 9–10 Ma.

2. Western equatorial to low latitude group (Figs. 36, 37, 38?, 39)

This groups consists of *Dorcadospyris alata* (Riedel) (Fig. 36), *Dorcadospyris dentata* Haeckel (Fig. 37), *Lithopera* (*Glomaria*) baueri Sanfilippo et Riedel ? (Fig. 38), and *Lithopera* (*Glomaria*) thornburgi Sanfilippo et Riedel (Fig. 39), which were distributed from the central- to western low-latitudes, western low-latitudes.

D. alata (Fig. 36) is considered to have occurred at low latitudes ($\leq 30^{\circ}$ N), except in the Mediterranean region (Sanfilippo et al., 1985). This species was found mainly in the low-latitude Pacific at 18–19 and 15–16 Ma and occurred along the western margin of the North Pacific at 12–13Ma. It was found along in the central equatorial Pacific at 9–10 Ma.

Sanfilippo et al. (1985) described the geographic distribution of *D. dentata* as similar to that of its descendant *D. alata*. We found that the occurrence patterns of *D. dentata* were similar to those of *D. alata* at 18–19 Ma (Fig. 37). However, *D. dentata* rarely occurred in the equatorial Pacific at 18–19 and 15–16 Ma.



Fig. 2. Distribution map of Calocycletta spp.

The *L. baueri–thornburgi* lineage diverged from *L. neotera* around the early Middle Miocene (Sanfilippo and Riedel, 1970). *L. baueri* (Fig. 38) occurred in the equatorial Pacific and along the western margin of the North Pacific at 15–16 Ma. At 12–13 Ma, it occurred sporadically in the equatorial Pacific. At 9–10 Ma, it was only found in the mid-latitude northwestern Pacific. *L. thornburgi* was found in late Middle Miocene samples from latitudes below 40° N in the Pacific, according to Nigrini and Sanfilippo (2001). This species shows a similar pattern to that of *L.* (*G.*) baueri: i.e., occurrences in the equatorial and western region with an exceptional occurrence in California at 12–13 Ma (Fig. 39).

3. Eastern low to mid-latitude group (Fig. 35?, early age of Fig. 51)

Pterocanium audax (Riedel) ? (Fig. 35) and the early distribution of *Phormostichoartus fistula* Nigrini (Fig. 51) tended to be distributed in the central to eastern low-latitudes and lower latitudes near California, and these two species is regarded as the eastern lower latitude group. Nigrini and Sanfilippo (2001) noted that *Pterocanium audax* (*=Lychnodictyum audax*) was found in samples from the middle Oligocene through the early Pliocene at latitudes below 40° N. This species (Fig. 35) was mainly found in the eastern



Fig. 3. Distribution map of Cyrtocapsella cornuta Haeckel.

equatorial Pacific. At 12–13 and 9–10 Ma, this species was known also from Japan.

4. Low to mid-latitude group (Figs. 2, 3, 6-15, 25, 26, 28, 31, later age of fig. 32, 42?, 43?, 46?, 47?, 52?, 53, 54, 56, 57-59?)

This group includes Calocycletta spp. (Fig. 2), Cyrtocapsella cornuta Haeckel (Fig. 3), Siphostichartus corona (Haeckel) (Fig. 6), Lithopera (Lithopera) renzae Sanfilippo et Riedel (Fig. 7), Anthocyrtidium ehrenbergi (Stöhr) (Fig. 8), Carpocanium spp. (Fig. 9), the Artiscins group (Fig. 10), Heliodiscus asteriscus Haeckel (Fig. 11), Lithopera (Lithopera) neotera Sanfilippo et Riedel (Fig. 12), Lamprocyclas spp. (Fig. 13), Pterocanium spp. (exclusive of P. audax, as discussed later) (Fig. 14), Pterocorys spp. (Fig. 15), Stichocorys delmontensis (Campbell et Clark) (Fig. 25), Stichocorys peregrina (Riedel) (Fig. 26), Spongurus cylindricus Haeckel (Fig. 28), Eucyrtidium spp. (Fig. 31), later distribution of Lamprocyrtis spp. (Fig. 32), Stichocorys armata (Haeckel) (Fig. 42), Stichocorys wolffii Haeckel ? (Fig. 43), Anthocyrtidium jenghisi Streeter ? (Fig. 46), Anthocyrtidium pliocenica (Seguenza) ? (Fig. 47), Botryostrobus miralestensis (Campbell et Clark) ? (Fig. 52), Cyrtocapsella japonica (Nakaseko) (Fig. 53), Lithocampe (?) yatsuoense (Nakaseko) (Fig. 54), Lithopera (Lithopera) bacca Ehrenberg (Fig. 56), Phormostichoartus corbula (Harting) ? (Fig. 57), Anthocyrtidium ophirensis (Ehrenberg) ? (Fig. 58), and *Theocorythium* spp. ? (Fig. 59) which were distributed from the low- to mid-latitude Pacific ($< 40^{\circ}$ N). These species tended to be distributed in this area through the examined age intervals, but were not always limited in this region.

Calocycletta spp. (Fig. 2) was distributed in low latitudes $(0-30^{\circ})$ at 18–19 Ma, but spread toward mid-latitudes (40° N) by 15–16 Ma. At 12–13 Ma, its distribution was separated into three areas: the low-latitude equatorial Pacific, the California margin and the north western marginal regions. This species was found only from the equatorial eastern Pacific at 9–10 Ma.

Cyr. cornuta (Fig. 3) appeared in the Aquitanian (Early Miocene) and disappeared in the Tortonian (Late Miocene; Nigrini et al., 2005). This species was widely distributed in the North Pacific but Site 883 at 18–19 Ma and expanded its distribution to the high-latitude regions, Alaskan region (15–16 Ma) and Kamchatka (12–13 Ma), but it was generally absent from the central North Pacific at these times. At 9–10 Ma, it was found from a few sites in the low-latitude Pacific and midlatitude central Pacific.

In the Early Miocene, *Siph. corona* (Fig. 6) evolved from *Siph. praecorona* Nigrini, and *Siph. praecoronata* diverged from *P. marylandicus* in the Late Oligocene (Nigrini, 1977). We found *Siph. corona* from the low-latitude Pacific at 18–19 Ma. At 15–16 and 12–13 Ma, *Siph. corona* was widely distributed in



Fig. 4. Distribution map of Phormostichoartus doliolum (Riedel et Sanfilippo).

the low-latitude Pacific, and the northern limit of its distribution apparently reached 30° N. This species disappeared in the midlatitude eastern Pacific at 9–10 Ma. Prior to its extinction in the Late Miocene (Nigrini, 1977), it was widely distributed in the low- to mid-latitude Pacific, except along the western margin of the Pacific at 6–7 Ma. There are no data along the western margin of the Pacific at 6–7 Ma.

L. renzae (Fig. 7) is presumed to have diverged from *Sti. diploconus* in the Middle Miocene and it disappeared in the late Middle Miocene (Sanfilippo and Riedel, 1970). The distribution of *L. renzae* tended to be separated into the equatorial Pacific, the northern west margin near Japan, and the California margin. Although this species is considered to have been extinct at 12.56 Ma in the low-latitude eastern Pacific (Nigrini et al., 2005) and at 11.79 Ma in the mid-latitude

western margin of the Pacific (Hayashi et al., 1999), we found that it occurred sporadically in the North Pacific at 9–10 Ma.

Anth. ehrenbergi, whose ancestor has not been determined, was extinct at approximately 3–4 Ma (Nigrini and Caulet, 1988). This species (Fig. 8) occurred in the low-latitude Pacific at 15–16. It expanded northward to 40° N at 12–13 Ma and populated the mid-latitudes until 6–7 Ma. The northern limit of the distribution of this species migrated to 30° N or lower latitudes expect for one site in Japan at 3–4 Ma.

Carpocanium spp. (Fig. 9) includes *Carpocanopsis* species herein, and is difficult to identify at the species level because of wide morphological variation. *Carpocanium* spp. was widely distributed from the equatorial Pacific to the mid-latitudes near 40° N from 18–19 to 1–2 Ma. We omitted the map at 9 – 10 Ma because the mapping is not finished yet for this time interval.



Fig. 5. Distribution map of Phormostichoartus marylandicus (Martin).

The Artiscins group (Fig. 10) comprises ellipsoidal coccodiscids with a double medullary shell connected to a cortical shell in the equatorial or subequatorial plane (De Wever et al., 2001). It includes the genera *Cypassis*, *Diartus*, and *Didymocyrtis*. This group was widely distributed in the North Pacific, except in the high-latitude region (> 40° N) from 18–19 to 1–2 Ma. *Heliodiscus asteriscus* (Fig. 11) shows distribution patterns similar to those of the Artiscins group.

L. neotera (Fig. 12) evolved from *L. renzae* at 12.7 Ma and evolved to *L. bacca* at approximately 11 Ma (Sanfilippo and Riedel, 1970; Sakai, 1980; Nigrini et al., 2005). Reference data (Table 3) show that this species already occurred in the low-latitude Pacific and around Japan at 15–16 Ma, although we did not encounter this species in the samples that we examined. Its distribution patterns were distinct from those of its ancestor, *L. renzae* (Fig. 7), and it was more widely distributed in the North Pacific, being absent from the high-latitudes (> 40° N).

The distribution of *Lamprocyclas* spp. was initially determined by Sanfilippo and Riedel (1992). We mapped its distribution at higher-resolution time intervals, considering plate motion. We found that *Lamprocyclas* spp. (Fig. 13) was very limited in the low-latitude western Pacific at 18–19 Ma. At 15–16 Ma, this genus disappeared from the low-latitude western Pacific and appeared instead in the eastern equatorial Pacific. It occurred from the low-latitudes to the mid-latitude

western Pacific at 12–13 Ma. At 9–10 Ma, the occurrence of this genus became separated into the mid-latitude Pacific around 30° N and the eastern equatorial Pacific. This genus was widely distributed from the low- to mid-latitude Pacific (< 40° N) from 6–7 to 1–2 Ma.

Pterocanium spp. (Fig. 14) were found from the eastern equatorial Pacific at 18–19 Ma, and it extended its distribution toward California at 15–16 Ma. The generic assignment followed Lazarus et al. (1985) and Sugiyama et al. (1992). This genus was widely distributed from the low- to mid-latitude Pacific at 12–13 and 9–10 Ma but absent from the western equatorial Pacific at 9–10 Ma. Since 6–7 Ma, the occurrence of this genus has been widely distributed from the low- to midlatitude Pacific (< 40° N).

Pterocorys spp. was initially determined by Sanfilippo and Riedel (1992) to have limited occurrence in the low-latitude Pacific Ocean and Indian Ocean in the Miocene, Pliocene, and Quaternary. *Pterocorys* spp. diverged from the genus *Albatrossidium* in the early Middle Miocene (Sanfilippo and Riedel, 1992). We found the oldest occurrence of this genus in the eastern equatorial Pacific at 15–16 Ma (Fig. 15). In contrast to the distribution map of Sanfilippo and Riedel (1992, fig. 10), we found *Pterocorys* not only in the mid-latitude western and eastern margins of the North Pacific, but also in the low-latitudes at 12–13 Ma. The distribution of this genus reached



Fig. 6. Distribution map of Siphostichartus corona (Haeckel)

a maximum of 40° N at 9–10 Ma, and the northern limit migrated slightly southward (30–35° N) at 6–7 and 3–4 Ma. At 1–2 Ma, according to the published date, *Pterocorys* spp. was distributed to 40° N but we found it only from the low-latitude Pacific at 1–2 Ma.

Sti. delmontensis (Fig. 25) occurred in the low-latitude Pacific at 21.14 Ma (Nigrini et al., 2005) and in the high-latitude Pacific at approximately 14 Ma (Morley and Nigrini, 1995). We found this species in the low-latitude Pacific and along the northwestern margin of the North Pacific at 18–19 Ma, followed by its wide expansion in the North Pacific at 15–16 Ma. This species disappeared from the high-latitude Pacific from 12–13 to 6–7 Ma. At 3–4 Ma it was patchily distributed in the mid-latitude northwestern and low-latitude eastern Pacific.

Sti. peregrina is a descendant of *Sti. delmontensis* and first appeared at approximately 14.9 Ma in the mid-latitude northwestern Pacific (Motoyama, 1999). The oldest record of this species is from the margin of the northwestern Pacific at 15–16 Ma (Fig. 26). It shows low- to mid-latitude distribution at time periods of 12–13, 6–7, 3–4 Ma. At 9–10 Ma, it expanded to high-latitudes while near disappeared from the low-latitudes.

Spg. cylindricus (Fig. 28) was found from the central to eastern North Pacific at 18–19 Ma and occurred in the equatorial Pacific at 15–16 Ma. It occurred in the equatorial zone and mid-latitude North Pacific at 12–13 Ma. After that, it spread its distribution but tended to be excluded from high-latitude sites.

Here, *Eucyrtidium* spp. (Fig. 31) includes *Stichopodium* 191



Lithopera (Lithopera) renzae Sanfilippo et Riedel

Fig. 7. Distribution map of Lithopera (Lithopera) renzae Sanfilippo et Riedel.

spp. in the sense of Petrushevskaya (1981), but we excluded *Eucyrtidium asanoi* Sakai from our description of the distribution of this group because the species showed a restricted distribution. *Eucyrtidium* spp. generally occurred over the entire North Pacific at 15–16 Ma. This species disappeared from both the low- and high-latitudes at 9–10 Ma and subsequently from the high-latitudes.

Stic. armata (Fig. 42) was mainly reported from the upper Lower Miocene in the low-latitude and North Pacific (e.g., Kling, 1973). Its known last appearance was at 14.6–14.8 Ma in the North Pacific (Kamikuri et al., 2004). This species was found sporadically near Japan, California, and the lowlatitude central Pacific at 12–13 Ma and was detected only in the western Pacific at 18–19 Ma. It spread in the low-latitude Pacific and near Japan and California at 15–16 Ma and was detected near Japan at 9–10 Ma.

Stic. wolffii (Fig. 43) first appeared in the low-latitude Pacific at 18.9 Ma (Nigrini et al., 2005) and its last appearance has not yet been precisely determined. This species was distributed in the western Pacific at 18–19 Ma, but we did not conclude that the species was absent in the eastern Pacific because of absence of data. This species was widely distributed in the Pacific, except in the low-latitude eastern Pacific, and high-latitude North Pacific at 15–16 Ma. Its distribution was limited to the low-latitude Pacific at 12–13 Ma. The distribution of *B. miralestensis* (Fig. 52) was limited at each time interval. For example, it was restricted to the low-latitude Pacific at 18–19 and 15–16 Ma, the low-latitude Pacific and northwestern Pacific at 12–13 Ma, and the western equatorial Pacific at 9–10 Ma.

Cyr. japonica (fig. 53) is considered to have evolved from *Clinorhabdus robusta* (Abelmann) (Takemura and Ling, 1998) or *Cyrtocapsella tetrapera* Haeckel (Sanfilippo and Riedel, 1970) in the early Miocene. This species had a single peak in abundance around Japan at 10.1 Ma before its extinction at ~9.9 Ma (Funayama, 1988; Sakai and Aita, 1994; Motoyama, 1999). The occurrence of this species was limited to part of the low- to mid-latitude North Pacific from 18–19 to 12–13 Ma. At 9–10 Ma, this species was restricted to the western to northeastern Pacific. It was reported to occur around Japan at 6–7 Ma (Table 3).

Lithocampe (?) *yatsuoense* (Fig. 54) was distributed in the low- to mid-latitude North Pacific at 18–19 and 15–16 Ma and disappeared from the low- to mid-latitude eastern North Pacific at 12–13 Ma. It occurred sporadically in the western North Pacific at 9–10 Ma.

5. Middle latitude group (Later age of fig. 33 and fig. 55)

We included the Lychnocanoma spp. (Fig. 33) that was

Anthocyrtidium ehrenbergi (Stöhr)



Fig. 8. Distribution map of Anthocyrtidium ehrenbergi (Stöhr)

present after 4 Ma and *Lithocampe chytra* Tan (Fig. 55). These groups were mainly distributed in the mid-latitude of the North Pacific. *Lychnocanoma magnacornuta* and *Lychnocanoma parallelipes* presented in the high-latitude in the North Pacific, as described later, and they were extinct prior to 4 Ma.

Lychnocanoma spp. was widely distributed in the lowlatitude and North Pacific from 18–19 to 9–10 Ma, except in the low-latitude western and eastern Pacific (Fig. 33). The distribution of *Lychnocanoma* spp. became contracted into the northwestern Pacific and equatorial eastern Pacific at 6–7 Ma. At 3–4 Ma, this group was only found from small regions in the mid-latitudes. At 1–2 Ma, this group was only found along the northwestern and northeastern margins of the mid-to-high latitude North Pacific. *L. chytra* (Fig. 55), tended to be present at low- to midlatitudes in the North Pacific

6. High latitude group (Figs. 16-18, 34, 40)

This group was distributed in the area higher than approximately 40° N and includes *Cycladophora sakaii* Motoyama (Fig. 16), *Lychnocanoma magnacornuta* Sakai (Fig. 17), *Lychnocanoma parallelipes* Motoyama (Fig. 18), *Eucyrtidium asanoi* Sakai (Fig. 34), and *Cycladophora cornuta* (Bailey) (Fig. 40).

The first appearance and last consistent occurrence of *Cyc. sakaii* were detected at 8.4 Ma and 2.2–2.4 Ma, respectively, in the northwestern Pacific (Kamikuri et al., 2004). This species **193**



Carpocanium spp.

Fig. 9. Distribution map of *Carpocanium* spp.



Fig. 10. Distribution map of the Artiscins group.



Fig. 11. Distribution map of Heliodiscus asteriscus Haeckel.



Lithopera (Lithopera) neotera Sanfilippo et Riedel

Fig. 12. Distribution map of Lithopera (Lithopera) neotera Sanfilippo et Riedel

already occurred near Japan and in the Gulf of Alaska at 9-10 Ma (Fig. 16). The southern limit of this species was placed along 35° N at 6-7 Ma. The distribution of this species was separated into the mid- to high-latitude northwestern Pacific and the California margin at 3-4 Ma.

Lyc. magnacornuta (Fig. 17) first appeared at 11.5–11.8 Ma and disappeared at approximately 7.0–7.3 Ma in the high-latitude North Pacific (e.g., Kamikuri et al., 2007). It occurred in the high-latitude Pacific at 12–13 and 9–10 Ma, and was found from the limited sites along the western to northern margin of the North Pacific at 6–7 Ma.

Lyc. parallelipes (Fig. 18) was a short-ranging species between 6.8–7.4 and 5.9–6.0 Ma in the northwestern Pacific (Motoyama, 1999; Kamikuri et al., 2004, 2007). At 6–7 Ma, this species was restricted within the northwestern Pacific.

Euc. asanoi (Fig. 34) occurred in the North Pacific from 15.2–15.4 to 12.7 Ma (Motoyama, 1999; Kamikuri et al., 2004, 2007). It was found only along the northwestern and northeastern margins of the North Pacific at 15–16 and 12–13 Ma, respectively.

Cyc. cornuta (Bailey) (Fig. 40) is a valid species for the invalid subspecies name "*Cycladophora davisiana* var. *cornutoides*" of Petrushevskaya (1967), as well as a senior synonym of the subspecies *Cycladophora davisiana* *cornutoides* Kling. We combine both of these "species" as *Cycladophora cornuta*. This species already occurred in the southwestern Pacific in the Late Eocene and occurred continuously worldwide in the Middle Miocene (Suzuki et al., 2009). It was distributed mainly in the mid- to high-latitude North Pacific from 6–7 to 1–2 Ma. Except for its isolated occurrence in the low-latitude eastern Pacific at 1–2 Ma, this species was generally absent from the low-latitude Pacific.

7. East group (early age of fig. 32 and fig. 44)

Lamprocyrtis spp.(Fig. 32) were distributed in the northeastern Pacific by 9 Ma and *Amphymenium amphystylium* Haeckel (Fig. 44) is likely to be present in the same region throughout the examined time interval.

The genus *Lamprocyrtis* spp. (Fig. 32) diverged from the genus *Lamprocyclas* in the late Early Miocene and occurred in the low-latitude and high mid-latitude Pacific from the Miocene to the Quaternary (Sanfilippo and Riedel, 1992). *Lamprocyrtis* spp. show an east-west contrast in its distribution from 18–19 to 9–10 Ma: i.e., it was present in the eastern part but nearly absent from the western part. Since 6–7 Ma, this genus has been commonly distributed in the North Pacific, except in the high-latitudes.



Fig. 13 Distribution map of Lamprocyclas spp.



Fig. 14. Distribution map of *Pterocanium* spp. (exclusive of *P. audax*)



Fig. 15. Distribution map of Pterocorys spp.



Fig. 16. Distribution map of Cycladophora sakaii Motoyama.

8. Cosmopolitan group (Figs. 19-24, 27, 29, 30, early age of fig. 33, 48?, 49, 50, and later age of fig. 51)

This group consists of *Cinclopyramis* spp. (Fig. 19), *Cornutella profunda* Ehrenberg (Fig. 20), *Cycladophora davisiana* Ehrenberg (Fig. 21), *Cyrtocapsella tetrapera* Haeckel (Fig. 22), *Saturnalis circularis* Haeckel (Fig. 23), the *Cyrtolagena pectinata* (Bailey) group (Fig. 24), *Xiphosphaerantha angelina* (Campbell et Clark) (Fig. 27), *Botryostrobus* spp. (Fig. 29), *Dictyophimus* spp. (Fig. 30), early distribution of *Lychnocanoma* spp. (excluding *Lychnocanoma magnacornuta* and *Lychnocanoma parallelipes*) (Fig. 33), *Artostrobus annulatus* (Bailey)? (Fig. 48), *Siphocampe arachnea* (Ehrenberg) group (Fig. 50), and later distribution of *Phormostichoartus fistula* Nigrini (Fig. 51).

Here, *Cinclopyramis* spp. (Fig. 19) includes the species belonging to *Bathropyramis*, *Enneapleuris*, *Peripyramis*, and *Sethopyramis*, as discussed in Suzuki et al. (2009). This genus was spread over the nearly entire North Pacific from 18–19 to 1–2 Ma, except at 15–16 Ma when it occurred at only two sites 572 and 883. In addition, it was not found along the northwestern margin of the North Pacific at 6–7 Ma.

We found Cornutella profunda (Fig. 20) only from Site 71

in the eastern equatorial Pacific at 18–19 Ma and the published date indicate its occurrence from Japan and California. Since 15–16 Ma, this species has been widely distributed over the North Pacific.

Cycladophora davisiana (Fig. 21) evolved from *C. sakaii* from 2.6 to 2.8 Ma in the North Pacific (Motoyama, 1997; Kamikuri et al., 2004, 2006). Unlike its ancestor (Fig. 16), *C. davisiana* was widely distributed in the North Pacific at 3–4 Ma, except in the high-latitude northwestern Pacific, and was distributed over the North Pacific at 1–2 Ma.

The oldest occurrence of *Saturnalis circularis* (Fig. 22) was recorded from the earliest Paleocene at Deep Sea Drilling Project (DSDP) Hole 208, Lord Howe Rise, Tasman Sea, as *Saturnulus* cf. *planetes* Haeckel (Dumitrica, 1973), and this species is still extant. This species was found only in the California region at 18–19 Ma; however, it occurred in the low- to high-latitude central to eastern Pacific at 15–16 Ma. Its occurrence was patchy from 12–13 to 6–7 Ma. Since 3–4 Ma, it has been distributed over the entire North Pacific.

The first appearance of *Cyrtocapsella tetrapera* nearly coincided with the boundary between the Oligocene and the Miocene (23.03 Ma) (Sanfilippo and Nigrini, 1995). The rapid decrease in abundance of this species at 12.5 Ma (Yanagisawa, 1999) has been used as a bioevent for stratigraphic correlation around Japan (e.g., Sakai and Aita, 1994). This species was



Lychnocanoma magnacornuta Sakai

Fig. 17. Distribution map of Lychnocanoma magnacornuta Sakai.



Fig. 18. Distribution map of Lychnocanoma parallelipes Motoyama.





Fig. 19. Distribution map of Cinclopyramis spp.



Fig. 20. Distribution map of *Cornutella profunda* Ehrenberg.



Cycladophora davisiana Ehrenberg

Fig. 21. Distribution map of Cycladophora davisiana Ehrenberg.

distributed throughout the low- to mid-latitude North Pacific from 18–19 to 12–13 Ma (Fig. 23). After its rapid decline at 9–10 Ma, it was found sporadically in the mid-latitude North Pacific and low-latitude central Pacific. This species was reported to have occurred near Japan at 6–7 Ma.

Cyrtolagena pectinata (Fig. 24) was distributed roughly over the entire North Pacific from 15–16 to 1–2 Ma, although it was absent from a few localities in each time period.

Xiphosphaerantha angelina (Fig. 27) occurred in the central to eastern Pacific at 18–19 Ma. It was widely distributed throughout the North Pacific at 15–16 and 12–13 Ma. At 9–10 Ma, it was absent from the western to northern margin of the Pacific. Since 6–7 Ma, this species has been distributed throughout the North Pacific. This species, however, are absent in the central part of the North Pacific at 3–4 Ma and 1–2 Ma.

Our description of distribution of the genus *Botryostrobus* spp. (Fig. 29) does not include *Botryostrobus miralestensis* (Campbell et Clark) because the species showed a very limited distribution. *Botryostrobus* spp. tended to occur throughout the North Pacific at 12–13 Ma and the later time intervals.

Dictyophimus spp. (Fig. 30) was found in the eastern equatorial Pacific at 15–16 Ma. After that, this genus gradually expanded its distribution north-westward, but it did not invaded into the southwest North Pacific during 13–6 Ma. It spread over the North Pacific during 4–1 Ma.

9. No significant group (Figs. 41 and 45)

A few species is unlikely to have particular distribution patterns: *Phormocyrtis alexandrae* O'Connor (Fig. 41) and *Anthocyrtella* (?) *callopsima* Caulet (Fig. 45). *Ph. alexandrae* (Fig. 41), an Early to Middle Miocene species (O'Connor, 1997), was found in limited numbers from the low-latitude Pacific at 18–19 Ma, but occurred separately in Japan and in the low-latitude eastern Pacific at 15–16 Ma. Only one locality is known in Japan at 12–13 Ma.

Discussion

The paleogeographic distributions of 58 selected taxa were mapped in the North Pacific from the Early Miocene (18–19 Ma) to the Middle Pleistocene (1–2 Ma) at intervals of \sim 1–2 m.y. using presence and absence data. These distribution patterns could be interpreted by environmental adaptations and changes in niches associated with the appearance of descendant species, but an extensive discussion of the implications is difficult without data on the species' abundances.

1. Possible interpretation of the distribution patterns

Several species had distributions that corresponded to latitudinal limits. For example, their distributions were often limited to the low-latitude Pacific below 30° N (Figs. 2–7), the low- to mid-latitude North Pacific below 40° N (Figs. 8–15), or the high-latitude North Pacific above 40° N (Figs. 16–18).

The geographic distributions in the Early Miocene to Pleistocene were commonly bounded by 30° and 40° N, respectively. According to a one-time snapshot of modern oceanographic vertical profiles at a selected meridian line from the World Ocean Circulation Experiment (WOCE; http://www. ewoce.org), the salinity changed abruptly at approximately 30° N and the potential temperature differed considerably at 40° N, probably related to differences in water mass. The changes in ocean salinity and temperature at present are highly significant in surface waters (< 200–500 m deep). At present, the North Pacific is divided into four latitudinal zones, i.e., the tropical, subtropical, transitional, and subarctic



Fig. 22. Distribution map of Saturnalis circularis Haeckel.



zones, by the Subtropical Front at $20^{\circ}-25^{\circ}$ N, the average Kuroshio Extension at $33^{\circ}-37^{\circ}$ N, and the Subarctic Front at $40^{\circ}-46^{\circ}$ N (Motoyama and Nishimura, 2005). However, past oceanographic conditions are not identical to those at present in the North Pacific (e.g., Kamikuri et al., 2008). The modern radiolarian fauna from the central North Pacific shows six geographical provinces that correspond with the following oceanographic features: the Subtropical, Transitional, and Subarctic zones, and the Kuroshio Extension, the Kuroshio Bifurcation, and Subarctic Front (Motoyama and Nishimura, 2005). By analogy with modern oceanographic conditions, we conclude that radiolarians of the Early Miocene–Pleistocene had separate niches at 30° and 40° N, probably because of the effect of the boundary in salinity and potential temperature. Our

data for the region of 20° – 30° N were so sparse that equatorial and low-latitude zones were not distinguished from the Miocene to the Pleistocene. However, at present, the tropical zone is distinguished by a relative abundance of radiolarians in surface sediments in the North Pacific (e.g., Kruglikova, 1966), suggesting the presence of distinct radiolarian assemblages in equatorial and low-latitude zones. *Dorcadospyris alata* (Fig. 36) and *Dorcadospyris dentata* (Fig. 37) were mainly distributed at low latitudes (< 20° – 25° N) and thus possibly show the range of the past tropic zone.

We recognized a high-latitude group that included *Cycladophora sakaii* (Fig. 16), *Lychnocanoma magnacornuta* (Fig. 17), and *Lychnocanoma parallelipes* (Fig. 18). Kamikuri et al. (2008) considered that subtropical and temperate water 207



Fig. 24. Distribution map of Cyrtolagena pectinata (Bailey) group.



Fig. 25. Distribution map of Stichocorys delmontensis (Campbell et Clark).

masses occupied the North Pacific in the Middle Miocene and that the subarctic water mass was not present at that time. The limited distribution of *Lyc. magnacornuta* in the highlatitude region (Fig. 17) implies the presence of different water masses in comparison with the mid-latitude water mass at that time. A time gap is recognized between the presence of *Lyc. magnacornuta* (9–10 Ma) and that of *Lyc. parallelipes* (~6–7 Ma) (Fig. 18), suggesting the presence of a different water mass in the higher latitude region prior to 9 Ma.

A total of 15 taxa were placed in the cosmopolitan group. *Cinclopyramis* spp. (Fig. 19) and *Cyrtolagena pectinata* (Fig. 24) are absent or rare above a water depth of 2500 m, i.e.,

the lower intermediate water around the Shatsky Rise (Sono et al., 2009), and at a water depth of 850 m, i.e., the upper intermediate water near Hokkaido (Suzuki et al., 2007). They are intermediate- or bottom-water dwellers. *Cornutella profunda* (Fig. 20), *Cycladophora davisiana* (Fig. 21), and *Saturnalis circularis* (Fig. 22) also dwell in the upper intermediate to deep water (> 200 m in depth) (Okazaki et al., 2004; Suzuki et al., 2007), and *Spongurus cylindricus* (Fig. 28) was trapped in the subsurface water (~100–200 m in depth) in the modern tropical western Pacific using a sediment trap (Yamashita et al., 2002), suggesting a mixed fauna of subsurface to deepwater dwellers. *Stichocorys peregrina* showed a distribution in the North Pacific



Fig. 26. Distribution map of Stichocorys peregrina (Riedel).

(Fig. 26), but its separation into two morphotypes, i.e., warmwater and cold-water forms, provides more precise information (e.g., Johnson and Wick, 1982). We presume that *Cyrtocapsella tetrapera* (Fig. 23), *Stichocorys delmontensis* (Fig. 25), and *Xiphosphaerantha angelina* (Fig. 27) were intermediate- or deepwater dwellers because they occurred not only in deep sea sediments, but also in shallower deposits in Japan.

There are locally distributed species from Miocene to Pleistocene. *Pterocanium audax* (Fig. 35), *Lithopera* (*Glomaria*) baueri (Fig. 38), *Lithopera* (*Glomaria*) thornburgi (Fig. 39), *Phormocyrtis alexandrae* (Fig. 41), and *Stichocorys wolffii* (Fig. 43) occurred in a portion of the low-latitude Pacific. *Eucyrtidium asanoi* (Fig. 34) showed a very limited distribution at higher latitudes. This species was extant from ~15.2–15.4 to ~12.7 Ma (e.g., Motoyama, 1999; Kamikuri et al., 2004, 2008), being just followed by the appearance of *Lyc. magnacornuta* (Fig. 17), which was distributed within the paleo-higher latitude water mass, as discussed above. Presumably, the paleo-higher latitude water mass appeared at 15.2–15.4 Ma or earlier. This prediction needs to be studied using high-resolution analyses for these particular time intervals.

Amphymenium amphistylium (Fig. 44), Artostrobus annulatus (Fig. 48), Siphocampe arachnea (Fig. 49), Siphocampe lineata (Fig. 50), and Phormostichoartus fistula (Fig. 51) were occasionally reported in the North Pacific, but their distributional data were limited. We found that these species had sporadic distributions in the North Pacific, although we only used presence/absence data. Abundance data for these



Fig. 27. Distribution map of Xiphosphaerantha angelina (Campbell et Clark).



Fig. 28. Distribution map of Spongurus cylindricus Haeckel.



Patrivastratus snn

Fig. 29. Distribution map of Botryostrobus spp.



 $100\,\mu m$

Fig. 30. Distribution map of Dictyophimus spp.



Fig. 31. Distribution map of *Eucyrtidium* spp.



Fig. 32. Distribution map of Lamprocyrtis spp.



Fig. 33 Distribution map of Lychnocanoma spp. (excluding Lychnocanoma magnacornuta and Lychnocanoma parallelipes).



Fig. 35. Distribution map of Pterocanium audax (Riedel).

taxa may provide insights into the paleoceanographic features that occurred within single water masses.

The regions of occurrence of *Botryostrobus miralestensis* (Fig. 52), *Cyrtocapsella japonica* (Fig. 53), and *Lithocampe* (?) *yatsuoense* (Fig. 54) changed through time. *Bot. mirabestnsis* moved from east to south, while *Lit.* (?) *yatsuoense* was first distributed in the low to mid-latitudes and then moved to the west. *Cyr. japonica* changed their distribution in the latest period before extinction.

2. Evolutionary relationships

The distributions of some taxa could have been altered not only because of environmental factors, but also because of changes in their competitive niches via evolutionary lineages. We recognized changes in the distributions of five phylogenetic lineages and groups: the *Cycladophora sakaii–Cycladophora davisiana* lineage (Figs. 16, 21), the *Cyrtocapsella tetrapera–Cyrtocapsella cornuta* lineage (Figs.



Fig. 36. Distribution map of Dorcadospyris alata (Riedel).

Dorcadospyris dentata Haeckel





Fig. 38. Distribution map of Lithopera (Glomaria) baueri Sanfilippo et Riedel.

Lithopera (Glomaria) thornburgi Sanfilippo et Riedel 18-19Ma 120' 150' 180'-150' -120' -90' 12-13Ma 13-13Ma 13-13Ma



Fig. 39. Distribution map of Lithopera (Glomaria) thornburgi Sanfilippo et Riedel.



Fig. 40. Distribution map of Cycladophora cornuta (Bailey).





Fig. 43. Distribution map of Stichocorys wolffii Haeckel.



Fig. 44. Distribution map of Amphymenium amphistylium Haeckel.

3, 23), the *Phormostichoartus fistula–Phormostichoartus corbula* lineage (Figs. 51, 57), the *Phormostichoartus marylandicus–Phormostichoartus doliolum–Siphostichartus coronata* lineage (Figs. 4, 5, 6), and the *Stichocorys* lineage (Figs. 25, 26).

Cycladophora sakaii–Cycladophora davisiana lineage: *Cyc. sakaii* (Fig. 16) first appeared in the Late Miocene from an unknown ancestor, and *Cyc. davisiana* (Fig. 21) diverged from *Cyc. sakaii* at 2.6–2.7 Ma (Motoyama, 1997), around the time of the strong cooling event in the Northern Hemisphere. *Cyc. sakaii* was mainly distributed in the higher latitude zone since 9–10 Ma and never expanded into other areas. In contrast, the descendant *Cyc. davisiana* spread to both the entire North Pacific and the southern oceans, i.e., the Indian Ocean and Atlantic Ocean (Lombari and Boden, 1985). *Cyc. sakaii* was reported from shallow sediments in Japan (e.g., Funakawa, 1993), suggesting that it is a shallow-water species, whereas extant *Cyc. davisiana* is an upper-intermediate- to deepwater species (Okazaki et al., 2005). The difference in the distributions of these species can be explained by the migration of *Cyc. davisiana* into the upper-intermediate to deep waters in the North Pacific around the time of the strong cooling event in the North Pacific.

Cyrtocapsella tetrapera–Cyrtocapsella cornuta lineage: These two species have been recorded from the Tertiary in Japan (e.g., Sakai and Aita, 1994). Atypical *Cyr. tetrapera* which has a constriction between the thorax and the abdomen looks similar to *Cyr. cornuta* (e.g., Hayashi et 223



Fig. 45. Distribution map of Anthocyrtella (?) callopsima Caulet.

al., 1999), but typical *Cyr. cornuta* is always larger than *Cyr. tetrapera* and has a more significant constriction between the thorax and the abdomen. We limited our designation of *Cyr. cornuta* to this typical form. *Cyr. tetrapera* (Fig. 23) first appeared at 22.65 Ma, and *Cyr. cornuta* (Fig. 3) diverged from *Cyr. cornuta* at 22.57 Ma (Sanfilippo and Riedel, 1970; Takemura and Ling, 1998; Nigrini et al., 2005). These species had overlapping distributions in the equatorial to low-latitude zones, but only *Cyr. tetrapera* was distributed in the higher latitude zone, suggesting difference in water preference of these two species. We predict that *Cyr. cornuta* lived near the surface (< 200–500 m in depth) in the equatorial and low-latitude zones of the North Pacific, whereas *Cyr. tetrapera* lived in the subsurface to bottom water (> 100–200 m and

deeper), suggesting a difference in niche.

Phormostichoartus fistula–Phormostichoartus corbula lineage: According to previous studies (Nigrini, 1977; Haslett, 2004), *Pho. fistula* had appeared by the Early Oligocene and disappeared by 3.47 Ma, and its descendant, *Pho. corbula*, diverged in the Middle Miocene and is extant in the present ocean. *Pho. corbula* (Fig.. 57) was found in samples from 12–13Ma. At 12–13 Ma, both species coexisted in the low- to mid-latitude eastern North Pacific, and their distributions only partly overlapped between 9–10 and 3–4 Ma in the equatorial to mid-latitudinal zone of the Pacific. This suggests that their ecological niches differed or they were ecological competitors. After the extinction of *Pho. fistula* (Fig. 51) at 3.47 Ma, *Pho. corbula* (Fig. 57) occupied



Fig. 46. Distribution map of Anthocyrtidium jenghisi Streeter.





the equatorial to mid-latitudinal zones of the North Pacific and probably expanded its niche into areas previously occupied by *Pho. fistula.*

Phormostichoartus marylandicus–Phormostichoartus doliolum lineage and Siphostichartus corona: For understanding of geographic distribution patterns of this lineage, the phylogenetic history should be reviewed at first. *Pho. marylandicus* appeared between the Late Eocene and the Early Oligocene and was extinct in the Late Miocene, whereas *Pho. doliolum* diverged from *Pho. marylandicus* in the late Middle Miocene (12–13 Ma) and disappeared at 3.82 Ma in the tropical oceans (Nigrini, 1977; Sanfilippo and Nigrini, 1998).

Prior to the appearance of *Pho. doliolum* (Fig. 4), *Pho. marylandicus* (Fig. 5) mainly occurred in the equatorial zone

from 18–19 to 15–16 Ma. Since 12–13 Ma, *Pho. doliolum* has shown a wider distribution than did its ancestor at 9–10 Ma. Prior to the appearance of *Pho. doliolum*, *Sip. corona* (Fig. 6) occurred in similar geographic areas to the phylogenetically close *Pho. marylandicus*. *Sip. corona* evolved from Oligocene *Sip. praecorona* whose ancestor is *Pho. marylandicus* (Nigrini, 1977). *Sip. corona* (Fig. 6) rapidly expanded its distribution from the equatorial zone at 18–19 – 15–16 Ma into the low-latitude zone at 12–13 Ma.

Their distribution changes could be explained the replacement of occupying species in a region. After several radiolarians, including *Cyr. tetrapera* (Fig. 23), declined in the northwestern Pacific at 12–13 Ma (e.g., Sakai and Aita, 1994), both *Sip. corona* (Fig. 6) and *Pho. doliolum* (Fig. 4) expanded their niches



Fig. 49. Distribution map of Siphocampe arachnea (Ehrenberg) group.



Fig. 50. Distribution map of Siphocampe lineata (Ehrenberg) group.

into the equatorial and low-latitude zones by 12-13 Ma.

Stichocorys lineage: We identified four *Stichocorys* species: *Sti. armata* (Fig. 42), *Sti. wolffii* (Fig. 43), *Sti. delmontensis* (Fig. 25), and *Sti. peregrina* (Fig. 26). The distributions of *Sti. armata* (Fig. 42) and *Sti. wolffii* (Fig. 43) overlapped in the equatorial to low-latitude zones in the North Pacific between 18–19 and 15–16 Ma. Before 12–13 Ma, *Sti. armata* (Fig. 42) disappeared in the North Pacific, whereas *Sti. wolffii* (Fig. 43) migrated into the low-latitude eastern Pacific, suggesting that an extinction event at 12–13 Ma affected these phenomena.

Sti. delmontensis (Fig. 25) and *Sti. peregrina* (Fig. 26) occurred in the equatorial to mid-latitudinal zones in the North Pacific during most of the time intervals examined. It is

noteworthy that *Sti. peregrina* (Fig. 26) mainly occurred in the equatorial to high latitude zones at 9–10 Ma, i.e., at relatively higher latitudes than at 12–13 and 6–7 Ma. These time intervals define the period of absence of the higher latitude water mass, and this interval is not only related with *Sti. delmontensis* and *Sti. magnacornuta*, but also the time gap in the ranges of two higher latitude species, *Lyc. magnacornuta* (Fig. 17) and *Lyc. parallelipes* (Fig. 18).

Casey (1982) proposed a paleo-distribution model of *Sti. delmontensis* (Fig. 25) and *Sti. peregrina* (Fig. 26) at 5.8–7 Ma in which warm-type *Sti. peregrina*, cold-type *Sti. peregrina*, and *Sti. delmontensis* were separately present in shallow waters (< 200 m in depth) of the equatorial to low-latitude zones, in shallow waters (< 200 m) of the mid-latitude



Fig. 51. Distribution map of Phormostichoartus fistula Nigrini.



Fig. 52. Distribution map of Botryostrobus miralestensis (Campbell et Clark).

zone, and in subsurface water (200–500 m in depth) from the equatorial to mid-latitudinal zones. If this model is true, different immigration patterns at 9-10 Ma might be interpreted by differences in the depths occupied by the two species.

3. Biostratigraphic interpretations

Many radiolarian bioevents have been recognized in the North Pacific, but their synchronicity varies from spontaneous to significant time-transgressive events (e.g., Spencer-Cervato et al., 1993). The compilation of biostratigraphic data from published species lists without illustrations occasionally leads to the creation of artificial time-transgressive events because of different concepts of radiolarian taxon identification by different authors. However, this effect can be eliminated by observing the original samples and only plotting results from publications that contain photographs of specimens.

Radiolarian specialists use different biostratigraphic schemes to determine depositional ages for the low-latitude Pacific (Sanfilippo and Nigrini, 1998) and the North Pacific (Motoyama, 1996; Kamikuri et al., 2004) because the radiolarian fauna differs significantly between these regions. Sanfilippo and Nigrini (1998) defined 19 radiolarian zones using biostratigraphic events from the Miocene through the Pleistocene. We examine 9 of these 19 events in the low-

latitude Pacific: the first occurrence (FO) of Calocycletta costata at 17.03 Ma, the FO of Sti. wolffii at 17.92 Ma, the evolutionary transition (ET) from Dorcadospyris dentata to Dorcadospyris alata at 15.66 Ma, the ET from Sti. delmontensis to Sti. peregrina at 6.71 Ma, the last occurrence (LO) of Pho. doliolum at 3.76-3.87 Ma, the LO of Pho. fistula at 3.42 Ma, the LO of Sti. peregrina at 2.74-2.78 Ma, the LO of Anthocyrtidium jenghisi at 2.40 Ma, and the LO of Xiphosphaerantha angelina (=Stylatractus universus) at 0.42 Ma. Calocycletta spp. (Fig. 2), Sti. wolffii (Fig. 43), Dor. dentata (Fig. 37), Dor. alata (Fig. 36), and Pho. doliolum (Fig. 4) were limited to the equatorial zones to some extent around the times of these bioevents, which are applicable only in very limited regions. Sti. delmontensis (Fig. 25) was nearly completely replaced by Sti. peregrina (Fig. 26) in the Messinian, but this replacement was a time-transgressive event resembling that at 7.1 Ma in the North Pacific (Motoyama, 1999) and that at 6.71 Ma in the low-latitude Pacific (Moore, 1995). This difference is explained by the occurrence of "relict" Sti. delmontensis (Fig. 25) at 3-4 Ma. Pho. fistula (Fig. 51) was sporadically distributed in the North Pacific at 3-4 Ma; thus, the LO of this representative species likely differs depending on the location. The distribution of Ant. jenghisi (Fig. 46) changed from the northwestern Pacific at 9-10 and 6-7 Ma to the low-latitude



Fig. 53. Distribution map of Cyrtocapsella japonica (Nakaseko).

and northwestern Pacific at 3–4 Ma. Therefore, the bioevents of this species must be interpreted with caution. In contrast to the other species, *Xip. angelina* (Fig. 27) occurred over the entire North Pacific from 15–16 to 1–2 Ma, except at 9–10 Ma, and the LO of *Xip. angelina* is a good biostratigraphic marker in the North Pacific (Hays and Shackleton, 1976; Sono et al., 2009). However, this bioevent is cautiously recognized in the low-latitude western Pacific and along the western margin of the Pacific because of this species' absence at 9–10 Ma.

The Middle Miocene to Pleistocene radiolarian zonation for the mid- to high-latitude North Pacific was updated by Kamikuri et al. (2004, 2008). These latitudes are roughly correlated with the transitional to higher latitude ocean climatic zones. Of the bioevents shown in Kamikuri et al. (2004: fig. 2), we discuss the following five events: the rapid decrease (RD) of *Cyr. tetrapera* at 12.5 Ma; the last consistent occurrence (LCO) of *Lyc. magnacornuta* at 9.0 Ma; the FO and LO of *Lyc. parallelipes* at 6.8–7.3 and 5.6 Ma, respectively; and the FO of *Cyc. davisiana* at 2.7–3.0 Ma. Although we have no species abundance data, *Cyr. tetrapera* (Fig. 23) disappeared abruptly from most regions of the North Pacific between 12–13 and 9–10 Ma. Except for in the central Pacific, the RD of this species in the mid- to high-latitude Pacific. This event has the potential for global correlation between the low-latitude and higher latitude Pacific. *Lyc. magnacornuta*

Fig. 55. Distribution map of *Lithocampe chytra* Tan.

Fig. 56. Distribution map of Lithopera (Lithopera) bacca Ehrenberg.

(Fig. 17) and *Lyc. parallelipes* (Fig. 18) were only found in the higher latitude zone, and thus their bioevents can only be applied to the higher latitude zone. *Cyc. davisiana* (Fig. 21) was widely distributed in the North Pacific and its FO can be easily recognized in the mid- to high-latitude North Pacific, as shown in previous studies (e.g., Kamikuri et al., 2004). We searched unsuccessfully for some index species, presumably because of sparse sampling intervals for *Dictyophimus bullatus* Morley et Nigrini and *Eucyrtidium matuyamai* Hays. In addition, we postponed the development of distribution maps for several species, including *Larcopyle pylomaticus* (Riedel) and *Lipmanella redondoensis* (Campbell et Clark), because of taxonomic uncertainty. in the mid-latitude North Pacific on the Shatsky Rise over the past 6.4 m.y. The cores that they studied were drilled from approximately $32^{\circ}13$ ' N and $158^{\circ}16$ ' E (ODP Site 1210), which is located in the low-latitude zone of our study. Sono et al. (2009) considered any biostratigraphic indicators recognized in the equatorial, mid-latitudinal, and higher latitude zones in the North Pacific, but barely recognized the FO of *Cyc. davisiana* at 2.84 ± 0.04 Ma, the LO of *Theocorythium vetulum* at 1.55 ± 0.05 Ma, or the LO of *Xip. angelina* at 0.44 ± 0.04 Ma. The time gaps of other bioevents exceeded 0.05 m.y. Except for *Tho. vetulum*, the results of Sono et al. (2009) are concordant with our results.

Sono et al. (2009) examined the radiolarian assemblages

Conclusions

Our distribution maps of selected radiolarian taxa were drawn using presence/absence data and indicate the distribution of each taxon, changes in the distributions through time through competition with species of the same phylogenetic group, and known radiolarian zonations in the North Pacific.

1. Distribution patterns

Shallow, western equatorial region: *Dorcadospyris alata* (Fig. 36) and *Dorcadospyris dentata* (Fig. 37). The probable water depth is surface water (< 200–500 m).

Shallow, equatorial region: *Phormostichoartus doliolum* (Fig. 4) and *Phormostichoartus marylandicus* (Fig. 5). The

probable water depth is surface water (< 200-500 m).

Shallow, equatorial and mid-latitude regions: Calocycletta spp. (Fig. 2), Cyrtocapsella cornuta (Fig. 3), Siphostichartus corona (Fig. 6), and Lithopera (Lithopera) renzae (Fig. 7), Anthocyrtidium ehrenbergi (Fig. 8), Carpocanium spp. (Fig. 9), Artiscins group (Fig. 10), Heliodiscus asteriscus (Fig. 11), Lithopera (Lithopera) neotera (Fig. 12), Lamprocyclas spp. (Fig. 13), Pterocanium spp. (exclusive of *P. audax*) (Fig. 14) and Pterocorys spp. (Fig. 15). The probable water depth is surface water (< 200–500 m).

Subsurface, equatorial and mid-latitude regions: *Stichocorys delmontensis* (Fig. 25), *Stichocorys peregrina* (Fig. 26) and *Spongurus cylindricus* (Fig. 28). Mixed fauna occurs from subsurface to bottom waters (100–200 m and deeper).

Anthocyrtidium ophirensis (Ehrenberg)

Fig. 58. Distribution map of Anthocyrtidium ophirensis (Ehrenberg).

Fig. 59. Distribution map of Theocorythium spp.

High-latitude region: *Cycladophora sakaii* (Fig. 16), *Eucyrtidium asanoi* (Fig. 34), *Lychnocanoma magnacornuta* (Fig. 17), and *Lychnocanoma parallelipes* (Fig. 18). The possible water depth is unknown.

Subsurface, cosmopolitan region: *Cyrtocapsella tetrapera* (Fig. 23) and *Xiphosphaerantha angelina* (Fig. 27), Mixed fauna occurs from subsurface to bottom waters (100–200 m and deeper).

Deep Cosmopolitan region: Cinclopyramis spp. (Fig.

19), *Cornutella profunda* (Fig. 20), *Cycladophora davisiana* (Fig. 21), *Saturnalis circularis* (Fig. 22), and *Cyrtolagena pectinata* group (Fig. 24). These occur in intermediate to deep water.

2. Competition hypothesis

We noted ecological competition and differentiated niches for species within phylogenetic lineages. *Cyc. sakaii* (Fig. 16) left its descendant *Cyc. davisiana* (Fig. 21) by immigration into the intermediate to deep waters of the Pacific. *Cyr. cornuta* (Fig. 3) and *Cyr. tetrapera* (Fig. 23) occurred at different water depths; the former was a surface-water dweller, whereas the latter was a subsurface- and to bottom-water dweller. The phylogenetically close species *Pho. marylandicus* (Fig. 5), *Pho. doliolum* (Fig. 4), and *Sip. corona* (Fig. 6) overlapped in their distributions before 12–13 Ma, and only *Pho. doliolum* (Fig. 4) expanded its niche into the equatorial and low-latitude zones at 12–13 Ma after the extinction of several radiolarian species. *Sti. delmontensis* (Fig. 25) and *Sti. peregrina* (Fig. 26) generally co-occurred in the same samples, but they may have lived at different depths.

3. Applicable area of radiolarian biozonations in the North Pacific

The distributions of most radiolarian taxa changed through time, and only two radiolarian bioevents, the FO of *Cyc. davisiana* and the LO of *Xip. angelina*, are applicable for global correlation from the equatorial to high-latitude North Pacific. Other bioevents for biozonation are applicable in only limited parts of the North Pacific. The zone of Sanfilippo and Nigrini (1998) is precisely applicable in the equatorial zone, whereas that of Motoyama (1996), which was updated by Kamikuri et al. (2004), is useful for the transitional to subarctic zones in the North Pacific. A new radiolarian zone is needed for the low-latitude zone.

The paleoceanographic, physical ecological, paleontological, and stratigraphic implications of the dynamic distribution patterns of most of the radiolarian taxa examined remain unaccountable. Nonetheless, our documentation of changes in species' distributions provides insight into the past North Pacific.

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Distribution map of Miocene-Pleistocene Radiolaria in the North Pacific

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