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Species composition and vertical distribution of diatoms occurring in a Japanese mangrove forest

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The species composition and vertical distribution of diatoms occurring on mangrove roots within the intertidal zone were studied in mangrove forests at Iriomote Island, Okinawa Prefecture. Among 116 taxa of diatoms belonging to 26 genera found there, the main dominant and subdominant species were *Achnanthes brevipes* var. *intermedia, Amphora luciae, A. tenerrima, Denticula subtilis, Navicula contenta, N. guluensis, N. pusilla, Nitzschia frustulum, N. hemistriata* and *Rhopalodia* sp. The vertical distribution of dominant diatoms on mangrove roots were shown as follows: *N. contenta* and *D. subtilis* on the uppermost part of the intertidal zone, *N. guluensis, N. hemistriata* and *Rhopalodia* sp. on the middle part, and *A. brevipes* var. *intermedia, A. luciae, A. tenerrima* and *N. pusilla* on the lower part. Comparisons with previous studies indicate that the species compositions of epiphytic and benthic diatoms on mangroves in this study are very similar to those of any other mangrove.

Key Index Words: diatoms—Iriomote Island—mangrove—species composition—vertical distribution.

Mangrove forests develop well but not extensively along the rivers and their mouths located in the Ryukyu and Satunan Islands, Japan. Mangrove forests serve as unique and specific habitats for benthic macro- and microalgae, which are exposed to water of varying salinity and/or desiccation, but are offered suitable substrata and interception of intensive sunshine by their stilt roots and canopies. In these habitats, benthic and epiphytic algae were usually much diverse and also abundant. Diatoms are one of the dominant members among them (RICARD and DELESALLE 1979). However, there are few taxonomic or floristic studies of diatoms associated with these Japanese mangrove forests. Almost all studies of diatoms in other mangrove regions have been confined to the large mangrove lagoons in the tropics such as in Puerto Rico (HAGELSTEIN 1938), in Louisiana (MAPELS 1983), in Florida (NAVARRO 1982), in Venezuela (REYES-VASQUEZ 1975), in Guadeloupe (RICARD and DELESALLE 1979), in Bahamas (SULLIVAN 1981), in Singapore and southern Malaysia (WAH and WEE 1988) and in the temperate regions of the southern hemisphere, such as in Australia (FOGED 1979).

The taxonomical and ecological researches for the macroalgae associated with Japanese mangrove forests have been carried out by TANAKA and CHIHARA (1984a, 1984b, 1985, 1987) and TANAKA (1987). They have shown that macroalgae are abundant on mangrove roots and have distinct zonate distributions in the intertidal zone.

We have undertaken a survey of diatom species composition and analyzed their vertical distribution in mangrove forests at Iriomote Island. This study represents the first report on Japanese mangrove diatoms, and should be valuable as a distributional record for more comprehensive work with this complex and diverse flora.

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Study sites and methods

In Iriomote Island of the Yaeyama Archipelago, Okinawa Prefecture, some small mangrove forests have developed in estuaries of the rivers, but they are the largest in Japan. They are dominated by Rhizophoracean trees, including the species of such genera as *Rhizophora, Kandelia* and *Bruguiera*. Their stilt or knee roots and pneumatophores offer suitable substrata for benthic diatoms.

Our main study sites were along the Shiiragawa (Shiira River) in Iriomote Island (Fig. 1). Eleven points of intervals of 200 m from the river mouth were previously set up by other Ryukyu University research staff (Fig. 1). The tide exerts its influence to the upper stream region of the river, about 2 km from the river mouth. In this region, the exchange of seawater with freshwater and their turbulence occur regularly twice a day throughout the year, and tidal range is 1.0–1.5 m near the river mouth. The mean high water (M.H.W.) reaches to the uppermost part of the stilt roots or higher. The lowermost part of the stilt roots is submerged even at mean low water (M.L.W.) (Fig. 2). Salinity of water at the study sites varied from fresh (0%) to marine (3%) depending on tide and freshwater current. However, a gradual variation of salinity was always recognizable at each study site.

Samples of the roots of mangrove trees and surface soils in the forest or river beds were taken from every study site on Apr. 21, 1982. For investigating the vertical distribution of benthic diatoms, some root samples from each point were sectioned to provide 10 cm segments. Diatoms on the segments were collected by toothbrush. All samples were cleaned by conventional methods (KOBAYASI and NAGUMO 1985). Samples were observed with both light and electron microscopes to identify the diatom species. The species composition and relative quantities of diatoms at each site were recorded by counting and identifying three hundred valves randomly selected from slides.

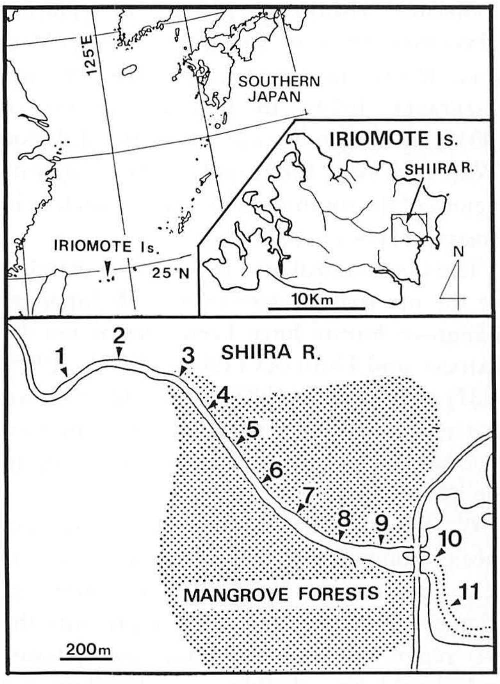


Fig. 1. Map of the study sites, showing the sampling points (1–11) indicated by arrow heads along the Shiira River.

Results

A total of 116 taxa including forma and varieties, in 26 genera, of epiphytic and benthic diatoms from all points are alphabetically listed in Table 1. The dominant four genera, in terms of number of taxa encountered, were *Navicula* (26), *Nitzschia* (18), *Amphora* (11) and *Achnanthes* (10). Representatives of epiphytic

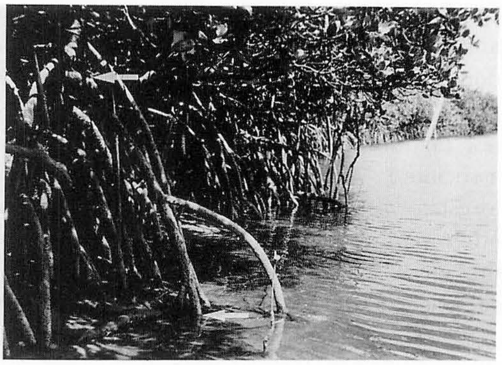


Fig. 2. A photograph of the Shiira River near point 8 showing a mangrove stilt root (arrows) from which diatoms were collected at low tide.

Table 1. List of diatom taxa found in the mangrove forest along the Shiira River.

Achnanthes amoena Hust.
- *brevipes* Ag. var. *brevipes*
- *brevipes* var. *intermedia* (Kütz.) Cl.
- *clevei* Grun.
- *delicatula* (Kütz.) Grun.
- *javanica* Grun.
- *kuwaitensis* Hendey
- *lanceolata* (Breb.) Grun.
- *longipes* Ag.
- *manifera* Brun.
- *oblongella* Östr.

Amphora angusta Greg. var. *angusta*
- *angusta* var. *ventricosa* (Greg.) Cl.
- *aponina* Kütz.
- *arenicola* Grun. var. *oculata* Cl.
- *holsatica* Hust.
- *luciae* Choln.
- *porita* Krasske
- *tenerrima* Al. *et* Hust.
- *turgida* Greg.
- *veneta* Kütz.
- 1 sp.

Auricula machutchoniae Giffen

Bacillaria paradoxa Gmel.

Biddulphia aurita (Lyngb.) Breb. et Gody.

Caloneis elongata (Grun.) Boyer
- *excentrica* (Grun.) Boyer
- *liber* (W. Sm.) var. *umbilicata* (Grun.) Cl.
- *samoensis* (Grun.) Cl.

Campylodiscus decorus Breb.
- *fastuosa* Ehr.

Cocconeis brevicostata Hust.
- *dirupta* Greg.
- *placentula* Ehr. var. *pseudolineata* Geitl.
- *scutellum* Ehr.

Denticula subtilis Grun.

Diploneis bombus Ehr.
- *gravelleana* Hagelst.
- *litoralis* (Donk.) Cl.
- *pseudovalis* Hust.
- *reichardtii* (Grun.) Heiden
- *smithii* (Breb.) Cl.

Entomoneis alata (Ehr.) Ehr.
- *paludosa* (W. Sm.) Reim. var. *paludosa*
- *paludosa* var. *subsalina* Cl.

Gomphonema clavatum Ehr.
- *pseudoaugur* L.-Bertalot
- *parvulum* (Kütz.) Kütz.

Gyrosigma spenceri (Grun.) Cl.

Mastogloia angulata Lewis
- *elliptica* (Ag.) Cl. var. *dansei* (Thwait.) Cl.
- *macdonaldii* Grey.
- *pumila* (Cl. et Möll.) Cl.
- *pusilla* Grun.
- *varians* Hust.

Melosira nummuloides (Dillw.) Ag.

Navicula acephala Herib.
- *cincta* (Ehr.) var. *leptocephala* (Kütz.) Grun.
- *contenta* Grun.
- *decussis* Östr.
- *digitoradiata* (Greg.) Ralfs
- *dissipata* Hust.
- *gregaria* Donk.
- *guluensis* Giffen
- *hastaeformis* Choln.
- *indicatrix* VanLand.
- *infaceta* Choln.
- *inserata* Hust. var. *inserata*
- *inserata* var. *undulata* Hust.
- *maculosa* Donk.
- *mannii* Hagelst.
- *mollis* (W. Sm.) Cl.
- *paeninsulae* Choln.
- *platyventris* Meist.
- *punctigera* Hust.
- *pusilla* W. Sm.
- *salinarum* Grun.
- *schroeteri* Meist. var. *escambia* Patr.
- *subvalida* Choln.
- 4 spp.

Nitzschia aerophila Hust.
- *debilis* (Arnott) Grun.
- *dissipata* (Kütz.) Grun.
- *fussiformis* Pantoc.
- *frustulum* (Kütz.) Grun.
- *granulata* Grun.
- *hemistriata* Hagelst.
- *lorenziana* Grun.
- *novaehollandiae* (Grun.) Grun.
- *obtusa* W. Sm. var. *scalpelliformis* Grun.
- *palea* (Kütz.) W. Sm.
- *panduriformis* Greg. var. *pustulata* Voigt
- *ponciensis* Hagelst.
- *pseudohungarica* Hust.
- *trybrionella* Hantz. var. *victoriae* (Grun.) Grun.
- 3 spp.

Opephora pacifica (Grun.) Petit

Pinnularia allansonii Choln.
- *mesolepta* (Ehr.) W. Sm.
- *subcapitata* Greg.

Pleurosigma salinarum Grun.

Rhopalodia gibberula (Ehr.) Müll.
- *operculata* (Ag.) Hakans.
- 1 sp.

Stauroneis pachycephala Cl.

Surirella armoricana Perag.
- *ovata* Kütz.

Synedra tabulata (Ag.) Kütz. var. *tabulata*
- *tabulata* var. *parva* (Kütz.) Hust.

Thalassiosira lacustris (Grun.) Hasle

Trachyneis aspera (Ehr.) Ehr.

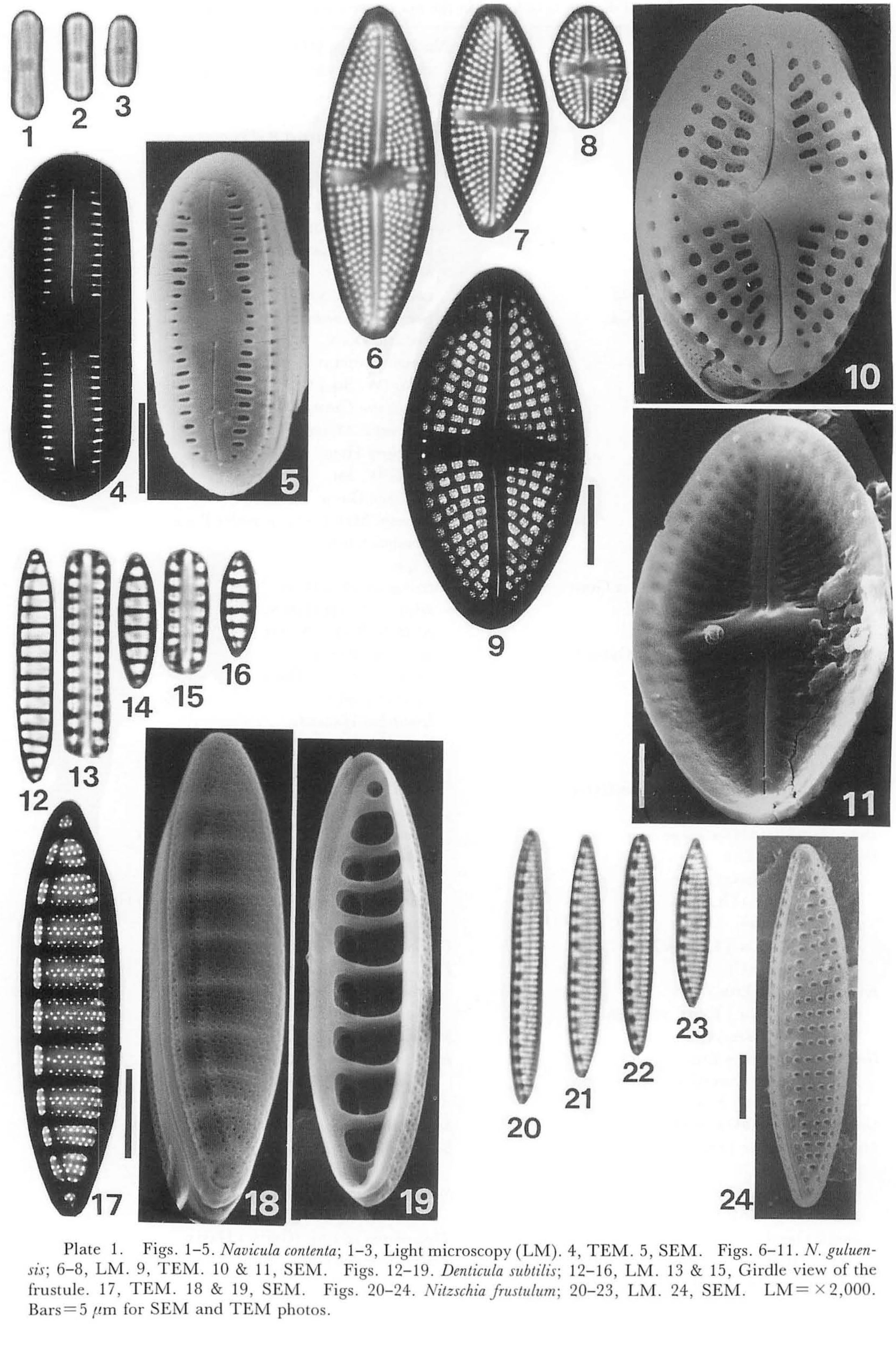


Plate 1. Figs. 1–5. *Navicula contenta*; 1–3, Light microscopy (LM). 4, TEM. 5, SEM. Figs. 6–11. *N. guluensis*; 6–8, LM. 9, TEM. 10 & 11, SEM. Figs. 12–19. *Denticula subtilis*; 12–16, LM. 13 & 15, Girdle view of the frustule. 17, TEM. 18 & 19, SEM. Figs. 20–24. *Nitzschia frustulum*; 20–23, LM. 24, SEM. LM = ×2,000. Bars = 5 μm for SEM and TEM photos.

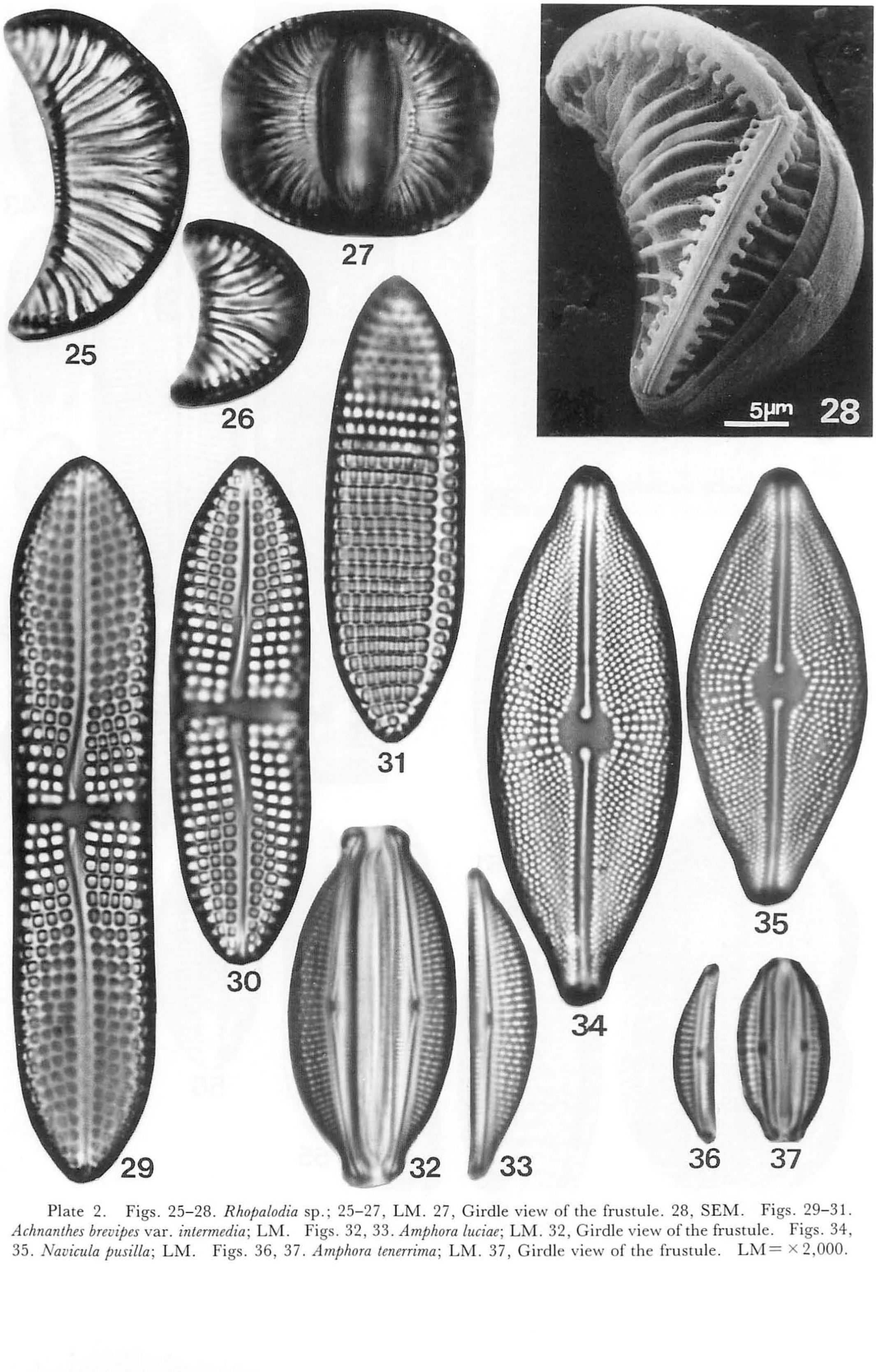
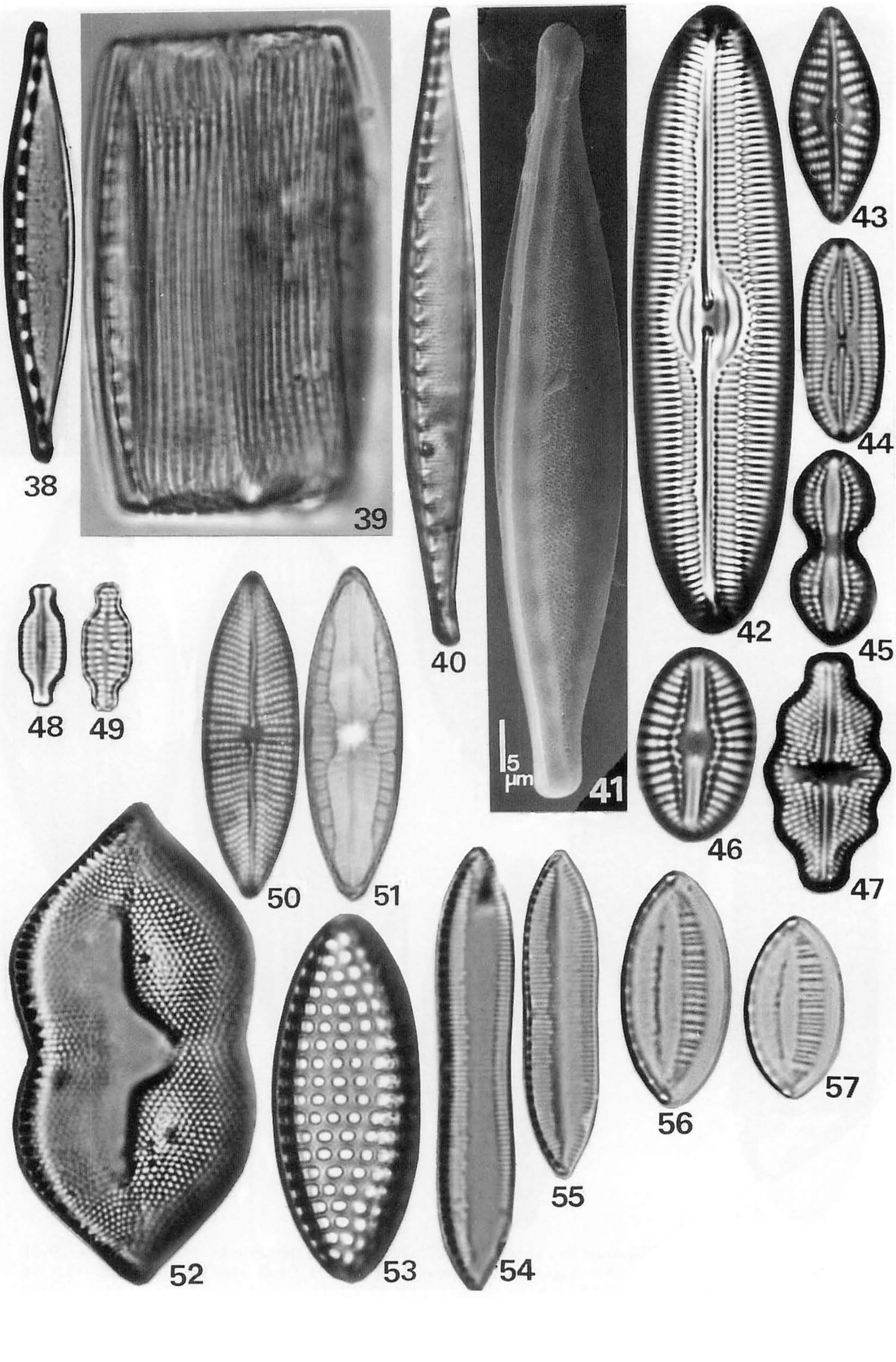


Plate 2. Figs. 25–28. *Rhopalodia* sp.; 25–27, LM. 27, Girdle view of the frustule. 28, SEM. Figs. 29–31. *Achnanthes brevipes* var. *intermedia*; LM. Figs. 32, 33. *Amphora luciae*; LM. 32, Girdle view of the frustule. Figs. 34, 35. *Navicula pusilla*; LM. Figs. 36, 37. *Amphora tenerrima*; LM. 37, Girdle view of the frustule. LM= ×2,000.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taxa on roots are as follows: *Achnanthes brevipes* AG. var. *intermedia* (KÜTZ.) CL. (1895, p. 193) (Pl. 2. Figs. 29-31), *Amphora luciae* CHOLN. (1960, p. 23, *f. 58-61*) (Pl. 2, Figs. 32, 33), *A. tenerrima* ALEEM *et* HUST. (1951, p. 16, *f. 3.*) (Pl. 2, Figs. 36, 37), *Denticula subtilis* GRUN. (1862, p. 547, *pl. 12, f. 36*) cf. KRAMMER & L.-BERTALOT (1988, p. 140, 141, *pl. 96, f. 1-9*) (Pl. 1, Figs. 12-19), *Navicula contenta* GRUN. (*in* V. H. 1884, p. 109) cf. KRAMMER & L.-BERTALOT (1986, p. 219, *pl. 75, f. 1-5*) (Pl. 1, Figs. 1-5), *N. guluensis* GIFFEN (1963, p. 238, *f. 70*) (Pl. 1, Figs. 6-11), *N. pusilla* W. SM. (1853, p. 52, *pl. 17, f. 145*) (Pl. 2, Figs. 34, 35), *Nitzschia hemistriata* HAGELST. (1938, p. 396, *pl. 8, f. 1*) (Pl. 3, Figs. 38-40), *N. frustulum* (KÜTZ.) GRUN. (*in* CL. *et* GRUN. 1880, p. 98) cf. KRAMMER & L.-BERTALOT (1988, p. 94, 95. *pl. 68, f. 1-19*) (Pl. 1, Figs. 20-24), *Rhopalodia* sp. (Pl 2, Figs. 25-28).

Common species appeared in every study site are represented in Pl. 3, Figs. 42-57. Almost all mangrove-associated diatoms including common species listed in Table 1 are regarded as brackish water or marine diatoms.

Aerobic species, *N. contenta* and *D. subtilis*, appeared dominantly or subdominantly at the upper portions of all study sites (Points 1-11).

In the lower stream regions of the river (Points 5-9), brackish species, *N. guluensis, N. hemistriata* and *Rhopalodia* sp., were dominant or subdominant at the upper to middle parts of the intertidal zone.

At the mouth and outlet of the river (Points 10, 11), the following marine species were dominant or subdominant at the lower to middle parts of the intertidal zone: *A. brevipes* var. *intermedia, A. luciae, A. tenerrima*, and *N. pusilla*.

Dominant or subdominant diatoms in the intertidal zones of all the examined sites ditributed in clear zonation. These vertical distribution pattern of diatom species attached to mangrove roots are summarized in Table 2; at the upper stream region of the mangrove (P-2), at the middle stream region (P-5), and at the lower stream region (P-8).

Discussion

The epiphytic and benthic diatom flora in the mangroves were more diverse than in estuaries without mangrove forests in the main island of Japan as shown in Table 3 (GOTOH 1978, 1979, 1986, MAYAMA and KOBAYASI 1982).

The vertical distribution of dominant and subdominant diatoms on mangrove roots showed a clear zonation (Fig. 3), similar to mangrove-associated macroalgae, as mentioned below (TANAKA and CHIHARA 1987). Of the dominant species occupying the upper part of intertidal zone, *N. contenta* GRUN. is a representative of the aerobic diatoms (HUSTEDT 1959). *A. brevipes* AG. var. *intermedia* (KÜTZ.) CL., *N. hemistriata* HAGELST. and *Rhopalodia* sp., which are dominant in the middle or lower part of intertidal

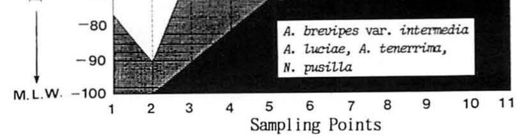

Fig. 3. Vertical distribution pattern of the dominant and subdominant diatoms on mangrove stilt roots at all sampling points. M.H.W., mean high water; M.L.W., mean low water.

Plate 3. Figs. 38–41. *Nitzschia hemistriata*; 38–40, LM. 39, Girdle view of the frustule. 41, SEM. Fig. 42. *Caloneis liber* var. *umbilicata*; LM. Fig. 43. *Navicula platyventris*; LM. Fig. 44. *N. punctigera*; LM. Fig. 45. *Diploneis gravelleana*; LM. Fig. 46. *D. pseudovalis*; LM. Fig. 47. *Navicula inserata* var. *undulata*; LM. Figs. 48, 49. *Achnanthes amoena*; LM. 48, Raphe valve. 49, Rapheless valve. Figs. 50, 51. *Mastogloia pusilla*; LM. Fig. 52. *Nitzschia panduriformis* var. *pustulata*; LM. Fig. 53. *N. granulata*, LM. Figs. 54, 55. *N. ponciensis*; LM. Figs. 56, 57. *N. debilis*; LM. LM = ×2,000.

Table 2. Vertical distribution of dominant and subdominant diatoms on mangrove stilt roots at the Shiira River. P-2, point 2; P-5, point 5; and P-8, point 8.

P-2

Relative tide level (cm)	Dominant species	Subdominant species
0		
	Denticula subtilis	*Navicula contenta*
−10		
	D. subtilis	*N. contenta*
−20		
	D. subtilis	*N. contenta*
−30		
	D. subtilis	*N. contenta*
−40		
	D. subtilis	*N. contenta*
−50		
	Nitzschia frustulum	*Denticula subtilis*
−60		
	N. frustulum	*D. subtilis*
−70		
	D. subtilis	*D. subtilis*
−80		
	D. subtilis	*Navicula guluensis*
−90		
	N. guluensis	*Nitzschia hemistriata*
−100		

P-5

Relative tide level (cm)	Dominant species	Subdominant species
0		
	Denticula subtilis	*Navicula contenta*
−10		
	D. subtilis	*N. contenta*
−20		
	D. subtilis	*N. contenta*
−30		
	Nitzschia hemistriata	*D. subtilis*
−40		
	N. hemistriata	*Navicula guluensis*
−50		
	N. hemistriata	*N. guluensis*
−60		
	N. hemistriata	*N. guluensis* *N. pusila*
−70		
	Navicula guluensis	*Nitzschia hemistriata* *Navicula pusila*
−80		
	N. pusila	*N. hemistriata* *Navicula gregaria*
−90		
	Achnanthes brevipes var. *intermedia*	*N. pusila*
−100		

P-8

Relative tide level (cm)	Dominant species	Subdominant species
0		
	Navicula contenta	*Denticula subtilis*
−10		
	D. subtilis	*Navicula guluensis* *N. hemistriata*
−20		
	D. subtilis	*N. guluensis* *N. hemistriata*
−30		
	D. subtilis	*N. hemistriata*
−40		
	N. hemistriata	*Rhopalodia* sp.
−50		
	N. hemistriata	*Rhopalodia* sp.
−60		
	Rhopalodia sp.	*D. subtilis* *Achnanthes brevipes* var. *intermedia*
−70		
	Rhopalodia sp.	*A. brevipes* var. *intermedia*
−80		
	Rhopalodia sp.	*A. brevipes* var. *intermedia*
−90		
	Amphora luciae	*A. brevipes* var. *intermedia* *Navicula pusila*
−100		
	A. tenerrima	*N. pusila*

zones, are commonly found as epiphytic or benthic species in marine waters. *N. hemistriata*, which was originally recorded from the sample collected from mangrove swamps in Martin Pena, Puerto Rico by HAGELSTEIN (1938), is also present. *D. subtilis* GRUN. is widely distributed in brackish environments such as estuaries and salt marshes, and is often associated with *Rhizoclonium* (GRUNOW 1862) or *Bostrychia* (GIFFEN 1970) which are common brackish macroalgae. These results show that some benthic diatoms from marine or brackish water are well adapted to the mangrove forest habitats exposed to waters with various salinities, and have their own niche or ecological status in the mangrove forest with close relation to other benthic macroalgae.

There is a limited work for diatom flora and its vertical distribution in brackish waters in the temperate and subtropical regions of Japan. Floristic studies of diatoms in

Table 3. A comparison of the number of taxa occurring in the mangrove forest and estuaries without mangrove forests in Japan.

Locality	Number of diatom taxa	Reference
Shiira-gawa, Mangrove, Okinawa Pref.	116	Present paper
Aono-gawa, Estuary, Shizuoka Pref.	108	MAYAMA & KOBAYASI (1982)
Kumano-gawa, Estuary, Wakayama Pref.	75	GOTOH (1986)
Yodo-gawa, Estuary, Osaka Pref.	86	GOTOH (1978)
Yodo-gawa, Estuary, Osaka Pref.	49	GOTOH (1979)

mangrove forests are also limited even in all over the world (FOGED 1979, HAGELSTEIN 1938, NAVARRO 1982, RICARD and DELESALLE 1979, WAH and WEE 1988). Community structure studies of mangrove diatoms have been confined to the USA (MAPLES 1983, SULLIVAN 1981). The dominant genera, *Achnanthes, Denticula, Navicula, Nitzschia* and *Rhopalodia*, found in this study are the same as reported by MAPLES (1983) as ephiphytes on pneumatophores of the black mangrove, *Avicenia germicans*, in a Louisiana salt marsh. In comparison to the epiphytic diatom flora associated with mangrove roots from Indian River by NAVARRO (1982), the dominant or subdominant species composition at Iriomote resembles to that of Indian River. These representative taxa found in the Japanese mangroves seem to be widely distributed in any tropical areas where mangrove forests are well developed.

According to TANAKA and CHIHARA (1987), the distribution of macroalgae on stilt roots and knee roots of mangrove trees in lower stream regions were divided into four main vertical zones; the *Rhizoclonium* zone, *Bostrychia* zone, *Caloglossa* zone, and *Catenella* zone. The vertical distribution pattern of macroalgae was not so clearly defined at the upper stream regions of the river, because the intertidal zone is too narrow for macroalgae of marine, brackish and fresh waters to be well separated. However, the dominant and subdominant diatoms showed clear zonation even in narrow spaces of the upper stream regions. Such typical zonation patterns of macroalgae in the lower stream regions fit well with those of diatoms as shown in Fig. 3.

The upper zone of *N. contenta* and *D. subtilis* generally corresponds to *Rhizoclonium* or *Bostrychia* zone, the middle zone of *N. guluensis, N. hemistriata* and *Rhopalodia* sp. to *Caloglossa* zone, and the lower zone of *Achnanthes* and others to *Catenella* zone. *D. subtilis* is well known to inhabit brackish water environments and to coexist with *Rhizoclonium* (GRUNOW 1862) or *Bostrychia* (GIFFEN 1970).

The vertical distribution of diatoms in the Japanese mangroves appears to be influenced by water movement, salinity and desiccation. The regular tide may be the main factor for the formation of vertical zonation of diatoms.

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南雲　保*・原　慶明**：本邦マングローブ林に生育するケイソウ類の種類組成と鉛直分布

沖縄県西表島の後良川マングローブ林内の上流から河口までの200 m毎に定めた11地点からマングローブの柱状根および周囲の表土を採取し，マングローブ林に生育するケイソウ類の種類組成と鉛直分布を調べた。その結果，26属に所属する116分類群の生育を確認した。また，全観察試料中，主要な優占および亜優占種は，*Achnanthes brevipes* var. *intermedia, Amphora luciae, A. tenerrima, Denticula subtilis, Navicula contenta, N. guluensis, N. pusilla, Nitzschia frustulum, N. hemistriata* and *Rhopalodia* sp. であった。また，それらは各調査地点で共通して，上部では *N. contenta* と *D. subtilis*, 中央部では *N. guluensis, N. hemistriata* と *Rhopalodia* sp., 下部では *A. brevipes* var. *intermedia, A. luciae, A. tenerrima* と *N. pusilla* が明瞭な帯状分布することを確認した。出現した種類の大半は，汽水あるいは海産の種類であり，マングローブ林の特異な塩分環境に良く適応している種組成と分布を示すと思われる。(*102 千代田区富士見1-9-20　日本歯科大学生物学教室，**305 茨城県つくば市天王台1-1-1　筑波大学生物科学系)