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Cover: A terminally resorbed maxillary tooth of iguanodontids (Ornithischia: Ornithopoda). The specimen is from the Kuwajima Formation, the Neocomian section of the Tetori Group, in Shiramine-mura, Ishikawa County, Ishikawa Prefecture, the west coast of Central Honshu, Japan (Shiramine-mura Board of Education, Coll. Cat. No. SBEI 001, 23 mm in dorsoventral length).

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995 Genetic variation within a dimorphic species, *Cryptopecten vesiculosus* (Bivalvia, Pectinidae)

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Abstract. An allozyme analysis of *Cryptopecten vesiculosus* was conducted to obtain biochemical evidence to determine whether the two discrete morphologic "phenotypes" represent dimorphism or two sympatric species. A total of 17 loci were extracted with polyacrylamide gel electrophoresis from specific tissues of the individuals collected from Sagami Bay, Japan. Of the 17 loci examined, seven (41.2%) were polymorphic, and avarage heterozygosity per individual was calculated at 0.20, indicating a high level of genetic variation in this species. The allozyme patterns are not statistically different between the two "phenotypes", confirming the previous interpretation based on morphologic and ecologic evidence that the two "phenotypes" represent discontinuous intrapopulational variants.

Key words: Dimorphism, random mating, genetic variation, allozyme, *Cryptopecten*

Introduction

Cryptopecten vesiculosus (Dunker) is a pectinid species known from lower sublittoral sandy bottoms of subtropical to temperate waters of the Northwest Pacific. It first appeared in the early Pliocene. During the Pliocene and early Pleistocene populations were monomorphic, but from the middle Pleistocene populations always bear two discrete "phenotypes" characterized by different modes of shell ornamentation. One phenotype has highly elevated and generally quadrate radial ribs, while the other has low and generally rounded radial ribs. They have been called "phenotype Q" and "phenotype R", respectively (Hayami, 1973; 1984).

Color polymorphism is common in molluscs, but the "dimorphism" of *C. vesiculosus* is unique, because the two "phenotypes" can easily be discriminated even in a worn or fragmental specimen owing to the solid nature of the shell surface ornamentation. "Phenotypic" frequency can therefore be determined also in fossil samples. Since this species occurs abundantly in post-early Miocene strata and present seas, the change of relative frequency of the two "phenotypes" in time and space was successfully traced using large population samples (Hayami, 1973, 1984).

The morphologic change through geologic time in this species is indeed remarkable and was interpreted as being the result of acquisition and spread of mutations by natural selection or random genetic drift (Hayami, 1973, 1984). Such "phenotypic" substitution without any intermediate forms was further considered as one of the possible causes for punctuated morphological evolution (Hayami and Ozawa, 1975).

Obviously, the above arguments concerning the evolutionary patterns of *C. vesiculosus* are based upon the assumption that the two "phenotypes" represent dimorphism within the species. This assumption relied upon the observations that the two "phenotypes" are strictly sympatric and have the same reproductive season, and that no significant difference beteen two "phenotypes" has been detected in other morphologic characters (Hayami, 1984). It is, however, important to ascertain the genetic relation between the two "phenotypes" by more direct methods, because random mating is a fundamental premise for the discussion of phenotypic substitution. Crossing experiments are difficult in view of the considerably long life cycle and lower sublittoral habitat of this species. In such a case, electrophoretic analyses of allozymes may be generally practical and effective.

In this paper, I intend to present a piece of evidence to decide the genetic relation between the two "phenotypes" based on an electrophoretic survey of allozymes. I also intend to show the extent of genetic variation in a population of *C. vesiculosus.*

Material and Methods

Specimens of *Cryptopecten vesiculosus* analyzed here were collected on 4th and 8th September 1994 by dredging operation at a locality (about 80 m deep) about 2 km west of Jogashima Islet, Sagami Bay, central Japan (the same locality as Sample Jg (1-26) by Hayami, 1984). The sampling was carried out to coincide with the season of maximum gonad development expected for this species,

Table 1. Buffer and tissue combinations in this analysis.

Enzyme	Abbreviation	Buffer	Tissue
Alcohol dehydrogenase	ADH	0.087M Tris-citrate ; pH 9.0	Gonad
Amylase	AML	0.087M Tris-citrate ; pH 9.0	Muscle
Glucose-6-phosphate dehydrogenase	G6PD	0.1M Tris-citrate ; pH 7.5	Mantle
Glucose-6-phosphate isomerase	GPI	0.025M Tris-citrate ; pH 7.5	Gonad
Guanine deaminase	GDA	0.025M Tris-citrate ; pH 7.5	Muscle
Lactate dehydrogenase	LDH	0.01M Na_2HPO_4-citrate ; pH 7.0	Gonad
Malate dehydrogenase	MDH	0.1M Tris-citrate ; pH 7.5	Gonad
Octanol dehydrogenase	ODH	0.087M Tris-citrate ; pH 9.0	Gonad
Peptidase-B	PEPB	0.045M Tris-citrate ; pH 8.6	Muscle
Phosphoglucomutase	PGM	0.045M Tris-citrate ; pH 8.6	Gonad
Phosphogluconate dehydrogenase	PGDH	0.01M Na_2HPO_4-citrate ; pH 7.0	Gonad
Superoxide dismutase	SOD	0.02M Tris-citrate ; pH 7.5	Gonad

because gonadal tissues offer a usful source of allozymes.

Specimens were transported alive to the Gelogical Institute, University of Tokyo, where they were frozen and kept at −80°C until processed for further analysis. An amount (0.05-0.1 g in wet weight) of either mantle, muscle or gonadal tissues of each individual was homogenized in a volume of 0.06 ml of grinding solution (0.01 M Tris, 0.1% (v/v) mercaptoethanol, 0.2% (v/v) glycerol ; pH 7.5) using a hand homogenizer. The homogenates were centrifuged at 15,000 rpm at 4°C for 5 minutes. The resulting supernatants were loaded onto vertical 15% polyacrylamide gels. Electrophoresis was carried out at 4°C for 3-6 hours under a constant voltage of 100 V. Gels except one for AML were then stained at 37°C following the methods described by Shimizu and Shimizu (1987) and Murphy *et al.* (1990). (Stain for AML : 0.35 M Tris-HCl, pH 8.0 30 ml ; starch 5 g ; 10 mg/ml diphosphopyridine nucleotide 2 ml ; 10 mg/ml 3-[4, 5-dimethyl-2-thiazolyl] 2, 5-diphenyltetrazolium bromide 2 ml ; 4 mg/ml phenazine methosulfate 1 ml.) Table 1 gives the combinations of buffers and tissues used for the separation of each enzyme. When multiple loci occur in an enzyme, the loci are numbered in order of decreasing anodal mobility.

Results

Of the 17 loci examined, seven (G6PD-1, G6PD-2, GPI-2, LDH, ODH, SOD-1 and SOD-2) in both "phenotype R" and "phenotype Q" were polymorphic, and the proportion of polymorphic loci (P) was therefore calculated as 0.41. All of the 17 loci, including the ten monomorphic loci (ADH, AML, GPI-1, GDA, MDH-1, MDH-2, PEPB, PGM, PGDH-1, PGDH-2) could be genetically interpreted. The results of allozymatic variation observed at each locus are summarized in Table 2. The examples of elecromorphs are shown in Figure 1. Heterozygosity at each locus is indicated in Table 3, and the average heterozygosity per individual was revealed as 0.20. The chi-squares tests of goodness of fit indicated that frequencies at each of the seven loci are consistent with Hardy-Weinberg expectations ($P>0.05$, Table 2), suggesting that all the individuals of each morphologic "phenotype" belong to a single randomly mating population.

Chi-squares tests for independence were employed to compare "phenotype Q" with "phenotype R" based on the determinations of allele frequencies at the seven variable loci. Null hypothesis was that no difference in allelic frequencies exists between "phenotype Q" and "phenotype R". In all the 17 loci, the null hypothesis was never rejected at the 95% confidence level ; this means that no significant genetic difference was observed between "phenotype Q" and "phenotype R", or that there is no evidence to support the presence of any reproductive isolation between the two "phenotypes".

Discussion

As mentioned befere, *C. vesiculosus* has been interpreted as an example of punctuated evolutionary change (at least in morphology) wihch transpired slowly in a large population without reproductive isolation. The allozyme data offer two kinds of information. One is that the two "phenotypes" of *C. vesiculosus* represent dimorphism within a species, and this is the assumption of that interpretation. The other is the level of heterozygosity in this population of *C. vesiculosus*.

It has been believed that there is a positive correlation between heterozygosities and effective population sizes (Nei, 1987). Heterozygosities of the species whose population sizes are very small, for example, *Mirounga angustirostris* (elephant seal) and *Acinonyx jubatus* (cheetah) are zero (Bonnell and Selander, 1974 ; O'Brien et al., 1985). Until now, heterozygosities in many species have been examined (Nevo, 1978 ; Nei and Graur, 1984), and in many species they are smaller than 0.2. Heterozygosity in a population of *C. vesiculosus* surveyed in this study (= 0.20) is not small as compared with those in other species

Table 2. Genotypic and allelic variation at 17 loci in a natural population of *C. vesiculosus*. N is the number of individuals.

Locus	Phenotype	N	Genotype										Allele			
			AA	AB	BB	AC	BC	CC	AD	BD	CD	DD	A	B	C	D
ADH	Q	30	30										60			
	R	30	30										60			
	Total	60	60										120			
AML	Q	30	30										60			
	R	30	30										60			
	Total	60	60										120			
G6PD-1	Q	30	9	12	6	2	1	0					32	25	3	
	R	34	10	12	6	3	3	0					35	27	6	
	Total	64	19	24	12	5	4	0					67	52	9	
G6PD-2	Q	30	2	7	9	1	10	1					12	35	13	
	R	30	5	8	10	1	6	0					19	34	7	
	Total	60	7	15	19	2	16	1					31	69	20	
GPI-1	Q	31	31										62			
	R	31	31										62			
	Total	62	62										124			
GPI-2	Q	31	3	13	15								19	43		
	R	31	3	14	14								20	42		
	Total	62	6	27	29								39	85		
GDA	Q	30	30										60			
	R	30	30										60			
	Total	60	60										120			
LDH	Q	31	1	9	21								11	51		
	R	32	2	11	19								15	49		
	Total	63	3	20	40								26	100		
MDH-1	Q	30	30										60			
	R	30	30										60			
	Total	60	60										120			
MDH-2	Q	30	30										60			
	R	30	30										60			
	Total	60	60										120			
ODH	Q	33	7	16	10								30	36		
	R	32	8	17	7								33	31		
	Total	65	15	33	17								63	67		
PEPB	Q	30	30										60			
	R	30	30										60			
	Total	60	60										120			
PGM	Q	31	31										62			
	R	32	32										64			
	Total	63	63										126			
PGDH-1	Q	30	30										60			
	R	30	30										60			
	Total	60	60										120			
PGDH-2	Q	30	30										60			
	R	30	30										60			
	Total	60	60										120			
SOD-1	Q	30	12	13	5								37	23		
	R	30	11	12	7								34	26		
	Total	60	23	25	12								71	49		
SOD-2	Q	31	2	1	1	2	0	2	4	5	6	8	11	8	12	31
	R	30	2	2	1	2	2	2	4	2	3	10	12	8	11	29
	Total	61	4	3	2	4	2	4	8	7	9	18	23	16	23	60

Table 3. Differences between observed and expected (from Hardy-Weinberg Law) numbers of genotypes tested for significance using chi-squares comparisons and between gene frequencies of "phenotype R" and "phenotype Q" tested by the same way. "He" is expected heterozygosity, and "Ho" is observed heterozygosity.

Locus	Phenotype	Allelic frequency (%)				Hardy-Weinberg Test		Q-R comparison		Heterozygosity		structures
		A	B	C	D	X^2	$X^2_{p=0.05}$	X^2	$X^2_{p=0.05}$	He	Ho	
ADH	Q	100								0	0	
	R	100								0	0	
	Total	100								0	0	
AML	Q	100								0	0	
	R	100								0	0	
	Total	100								0	0	
G6PD-1	Q	53.3	41.7	5.0		0.50	7.81			0.53	0.50	monomer
	R	51.5	39.7	8.8		0.87	7.81			0.57	0.53	
	Total	52.3	40.6	7.0		1.07	7.81	0.71	5.99	0.56	0.52	
G6PD-2	Q	20.0	58.3	21.7		2.55	7.81			0.57	0.60	monomer
	R	31.7	56.7	11.6		4.16	7.81			0.57	0.50	
	Total	25.8	57.5	16.7		6.69	7.81	3.40	5.99	0.57	0.55	
GPI-1	Q	100								0	0	
	R	100								0	0	
	Total	100								0	0	
GPI-2	Q	30.6	69.4			0.01	3.84			0.43	0.42	monomer
	R	32.3	67.7			0.03	3.84			0.44	0.45	
	Total	31.5	68.5			0.01	3.84	0.04	3.84	0.43	0.44	
GDA	Q	100								0	0	
	R	100								0	0	
	Total	100								0	0	
LDH	Q	17.7	82.3			0.00	3.84			0.29	0.29	dimer
	R	23.4	76.6			0.06	3.84			0.36	0.34	
	Total	20.6	79.4			0.06	3.84	0.62	3.84	0.33	0.32	
MDH-1	Q	100								0	0	
	R	100								0	0	
	Total	100								0	0	
MDH-2	Q	100								0	0	
	R	100								0	0	
	Total	100								0	0	
ODH	Q	45.5	54.5			0.02	3.84			0.50	0.48	dimer
	R	51.6	48.4			0.13	3.84			0.50	0.53	
	Total	48.5	51.5			0.02	3.84	0.49	3.84	0.50	0.51	
PEPB	Q	100								0	0	
	R	100								0	0	
	Total	100								0	0	
PGM	Q	100								0	0	
	R	100								0	0	
	Total	100								0	0	
PGDH-1	Q	100								0	0	
	R	100								0	0	
	Total	100								0	0	
PGDH-2	Q	100								0	0	
	R	100								0	0	
	Total	100								0	0	
SOD-1	Q	30.6	69.4			0.01	3.84			0.43	0.42	monomer
	R	32.3	67.7			0.03	3.84			0.44	0.45	
	Total	31.5	68.5			0.01	3.84	0.31	3.84	0.43	0.44	
SOD-2	Q	17.7	12.9	19.4	50.0	4.48	12.59			0.66	0.58	monomer
	R	20.0	13.3	18.3	48.3	5.97	12.59			0.68	0.50	
	Total	18.9	13.1	18.9	49.1	6.57	12.59	0.12	7.81	0.67	0.54	
						Average heterozygosity per individual =				0.21	0.20	

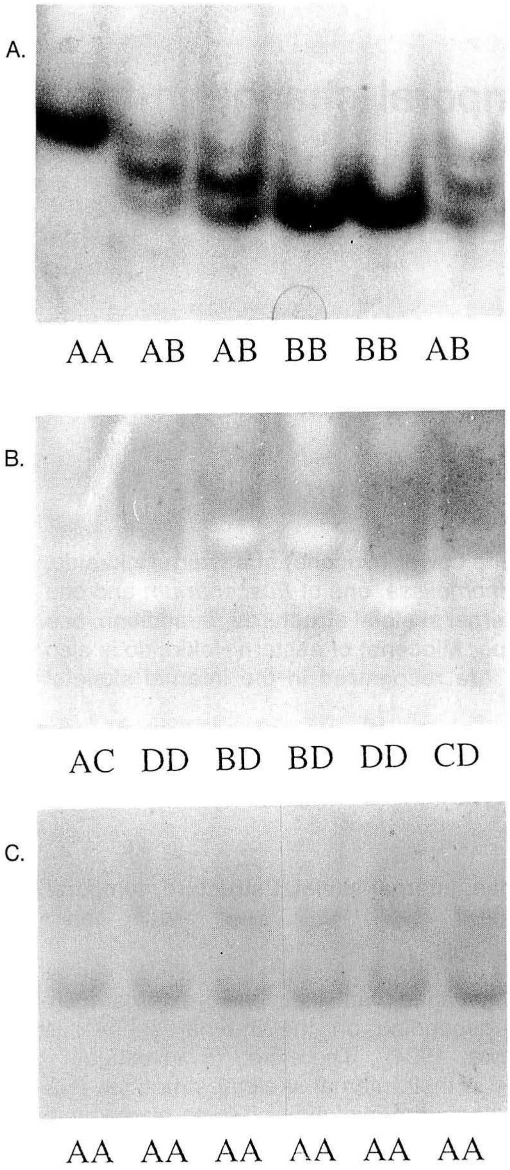

Figure 1. Examples of three types of enzyme banding patterns in *C. vesiculosus*.

A : Polymorphic locus of dimer (This example is ODH). Homozygotes are indicated by one band and heterozygotes by three. B : Polymorphic locus of monomer (This example is SOD-2). Homozygotes are indicated by one band and heterozygotes by two. C : Monomorphic locus (This example is MDH). Two loci are indicated. Upper bands represent MDH-1 and lower bands represent MDH-2.

hitherto investigated.

From this study it becomes clear that the two phenotypes of *C. vesiculosus* represent a dimorphism. However, the genetic background of this discontinous morphologic variation is still obscure. Consequently, the interpretation that phenotypic substitution results from the accumulation of a sigle mutant gene still remains tentative, and it is a problem awaiting solution whether the accumulation was driven by natural selection or random genetic drift (or by any other causes). Further genetic investigations are required, and such studies would greatly contribute to the development of evolutionary theory.

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996 Intrageneric variation and temporal change in the internal skeletal structure of plagiacanthids (Radiolaria) from Hokkaido, Japan

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Abstract. From the Kawakami Group (the Upper Oligocene to Lower Miocene) of eastern Hokkaido, five new species of Clathromitrinae, including three of *Corythomelissa*, one of *Euscenarium* and one of *Lithomelissa*, are described, placing emphasis on their internal skeletal structure. In addition, one species of Clathromitrinae from the Taiki Formation (the Upper Miocene) of eastern Hokkaido is also examined. Some intraspecific and intrageneric variations are recognized in the internal skeletal structure of *Corythomelissa*.

The intrageneric variations have three tendencies over time : (1) the prolongation of *L-Rd* ; (2) the rising of connecting archers on the dorsal side of the shell ; (3) the decline of *A′*. These intrageneric variations show a general trend through Late Oligocene to Late Miocene time which represents the evolutionary lineage of *Corythomelissa*.

Key words : Late Oligocene to Late Miocene, Plagiacanthidae, internal skeletal structure, temporal change, evolutionary lineage

Introduction

Evolutionary lineages of Cenozoic radiolarians have been examined by many investigators (e.g. Riedel and Sanfilippo, 1970, 1971 ; Moore, 1972 ; Foreman, 1973 ; Sanfilippo and Riedel, 1973, 1982 ; Goll, 1979 ; Lazarus *et al.*, 1985 ; Sanfilippo, 1990) mainly through materials provided by the Deep Sea Drilling Project. Recognition of these lineages was based mainly on temporal changes in external structures of radiolarian shells. Concerning the family Plagiacanthidae, Goll (1979) determined the evolution of the genus *Callimitra* based on the morphological change of external shells through time. It was revealed by some authors (e.g. Swanberg and Bjørklund, 1987 ; Nishimura, 1990) that the internal skeletal structure of Nassellaria is formed during early ontogeny. Although the value of internal skeletal structures for nassellarian taxonomy has been demonstrated by many investigators (Riedel, 1967, 1971 ; Petrushevskaya, 1971a, 1971b, 1975, 1981 ; Takemura, 1986 ; Nishimura, 1990 ; Sugiyama, 1993, 1994), the temporal changes of these structures have not been studied yet.

It is easy to observe the internal skeletal structure of plagiacanthids because most internal skeletal elements are not hidden within the shell. The external skeletons are highly varied, with their basic external morphologies usually depending on the internal skeletal structures (Funakawa, 1994). Therefore, to investigate temporal changes in their internal skeletal structures is a suitable way to clarify the evolution of some plagiacanthids.

In this paper, five new species of the Clathromitrinae are described from Upper Oligocene to Lower Miocene strata putting special emphasis on their internal skeletal structures. In addition, the internal skeletal structure of one species of *Corythomelissa* from Upper Miocene strata is examined. Detailed examinations of internal skeletal structures of the above-mentioned species show intergeneric variations in their internal skeletal structures occurring within the stated time interval. The author proposes the evolutionary trends of four species of *Corythomelissa* based on this temporal change in their internal skeletal structures.

Geological setting and materials

The Kawakami Group (Mitani *et al.*, 1959) is distributed in Hombetsu, Morawan and Kamiashoro regions, eastern Hokkaido, Japan (Figure 1). Along the Morawan River route, the Kawakami Group is well exposed (Figure 2) and is subdivided into three formations, the Hombetsuzawa,

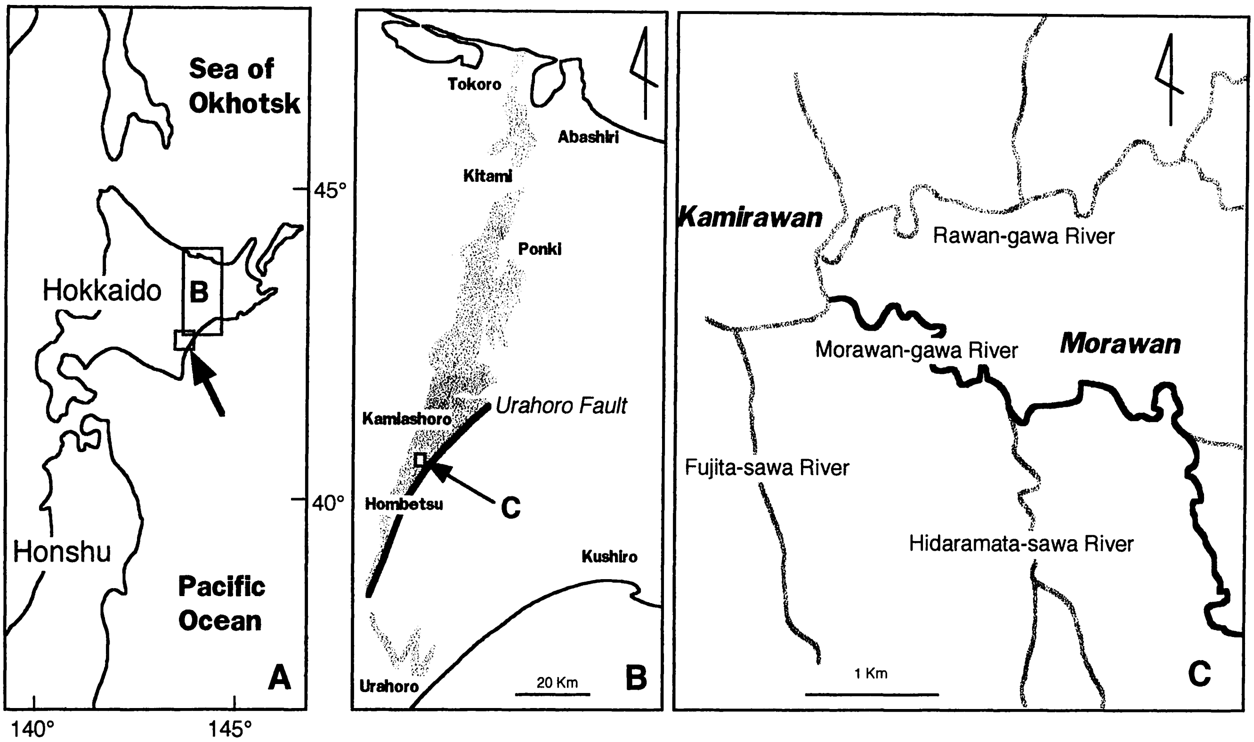

Figure 1. Index maps. (**A**) Northeast Japan around Hokkaido. Arrow points to Toyokoro Hills region (Funakawa, 1994). (**B**) Distribution of the Upper Oligocene to Lower Miocene sediments in eastern Hokkaido (after Matsui and Ganzawa, 1987). (**C**) River system around Morawan River.

Morawan and Kiroro Formations in ascending order (Inoue and Suzuki, 1962). The Hombetsuzawa and Morawan Formations are characterized by numerous biosiliceous layers. The Morawan Formation is subdivided into four members; the lower platy shale, the Kamirawan Sandstone, the middle hard shale and the upper tuffaceous mudstone members. The Kiroro Formation is characterized by sandstone and non-siliceous siltstone, and is subdivided into two members; the lower sandstone and the upper siltstone members. Calcareous nodules yielding well preserved radiolarians are contained in the biosiliceous layers of the Morawan Formation and siltstone layers of the Kiroro Formation.

The age of the Kawakami Group is based on a combination of radiometric, fission track and biostratigraphical data (Figure 3). Matsui and Ganzawa (1987) presented chronological data by K-Ar and fission track dating. Saito *et al.* (1988) reported Late Oligocene diatoms and radiolarians from the lower platy shale member of the Morawan Formation. From the upper siltstone member of the Kiroro Formation, a diatom species, *Thalassiosira fraga*, occurs while *Actinocyclus ingens* is absent (Ariga, pers. comm.). This fact indicates that the age of the upper part of this member is between 19.5 Ma and 16.8 Ma (Akiba, 1986). These data indicate that the Kawakami Group was deposited during Late Oligocene to Early Miocene time.

In this study, seven calcareous nodule samples from four horizons are examined. These horizons are shown in Figure 3.

In addition to the above-mentioned samples, the author examined diatomaceous siltstone samples from the Upper Miocene Taiki Formation (Yamaguchi and Satoh, 1989; Yamagishi *et al.*, 1990). These samples were collected along the Oikamanai River and Noyaushi River routes (Funakawa, 1993; 1994) in the Toyokoro Hills region, eastern Hokkaido (Figure 1). Localities of radiolarian samples are given by Funakawa (1993, 1994). All samples are included within the Upper Miocene interval from the *Denticulopsis dimorpha* Zone through *Thalassionema schraderi* Zone of Koizumi (1985).

Depository of type specimens is in the Department of Geosciences, Faculty of Science, Osaka City University.

Notes for terminology of internal skeletal structure

Most skeletal terms follow Petrushevskaya (1968) and Dumitrica (1991): **MB** (median-bar), **A** (apical spine), **D** (dorsal spine), **V** (ventral spine), **L** (right and left lateral spines) and **l** (right and left secondary lateral spines); notation of connecting arch is a combination of two abbreviations of internal elements connecting together (i.e. **AL** is an arch connecting **A** and **L**, **D**-**AL** is an arch connecting **D** and **AL**). Following Funakawa (1995), several internal spicules, **A, V, D** and two **L** form several horns, feet and ribs and these outside skeletal elements are the prolongations of these internal skeletal elements: **A** sometimes forms an apical rib in the shell wall and an

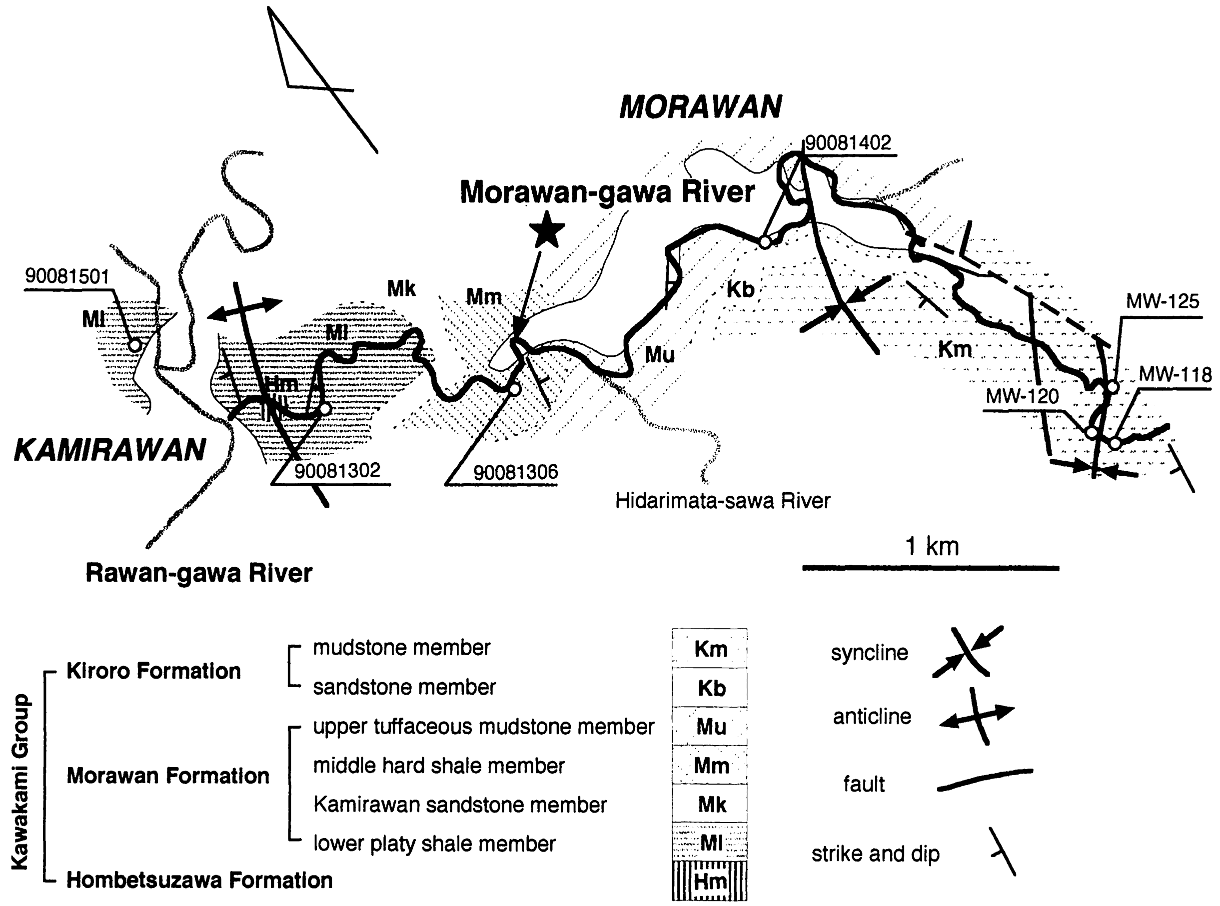

Figure 2. Sample localities along Morawan River Route. Stratigraphy and geological structure are based on Inoue and Suzuki (1962). Star indicates the sample locality of K-Ar dating reported by Matsui and Ganzawa (1987).

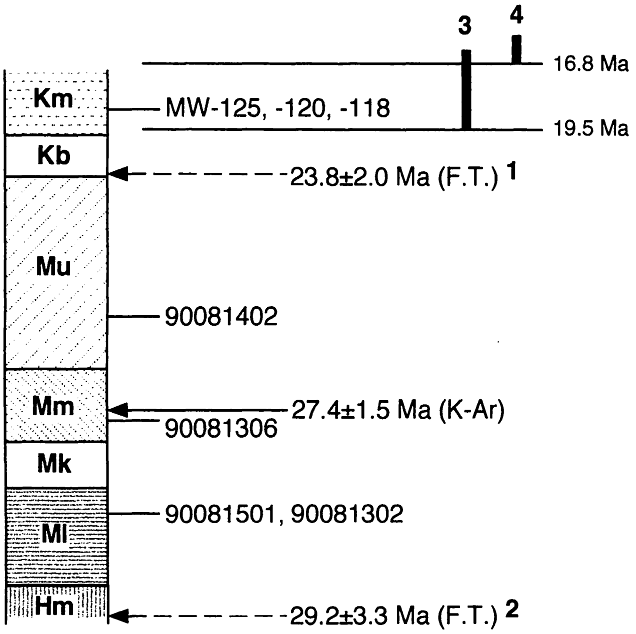

Figure 3. Simplified stratigraphic column with horizons of radiolarian samples. Abbreviations are the same as those in Figure 2. Potassium argon (**K-Ar**) and Fission Track (**F.T.**) ages are from Matsui and Ganzawa (1987). Arrow with solid line shows the datum from Morawan River Route. Arrows with dotted lines show data from other regions than Morawan. **1**: Ponki region, the base of Tsubetsu Formation correlated to the base of the Kiroro Formation. **2**: Hombetsu region, base of the Hombetsuzawa Formation. Diatom occurrences are provided by Ariga (pers. comm.); **3**: *Thalassiosira fraga*, **4**: *Actinocyclus ingens*. The first appearance datums of these two diatoms are based on Akiba (1986).

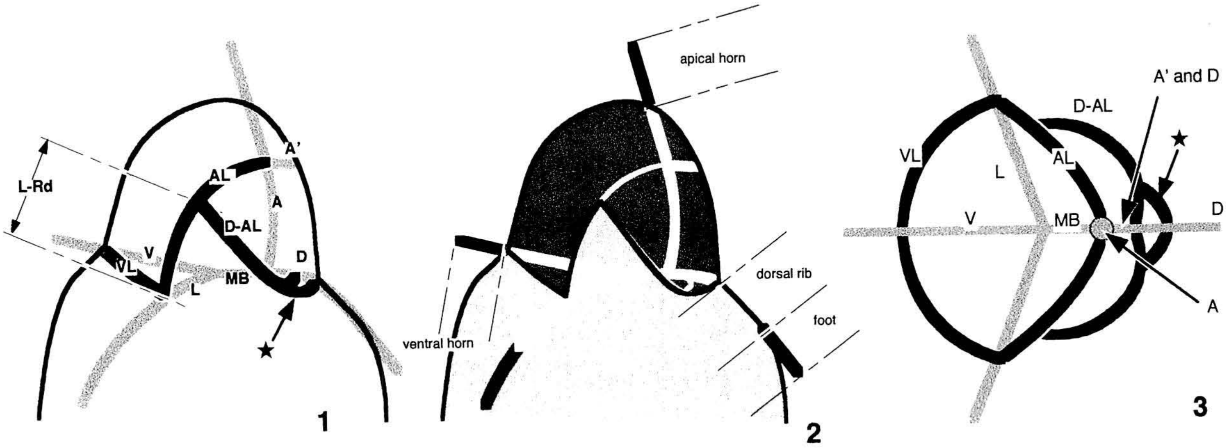

Figure 4. Schematic illustrations of internal skeletal structure of *Corythomelissa*. **1** : Internal skeletal structure of left lateral view. **2** : Subdivision of two segments with internal skeletal structure. **3** : internal skeletal structure of apical view. Stars indicate the branches of **D** and **L**, and other abbreviations are explained in the text.

1 and **3** : Grey lines show internal spicules and thick black lines do connecting arches. **2** : Thick lines show internal spicules (white) and their prolongations in and outside the shell wall (black). Weak lines show connecting arches inside the shell (white) and in the shell wall (black). Broken line shows outline of shell. Dark grey part indicates the first segment and light grey part does the second segment.

apical horn outside the shell ; **V** sometimes forms a ventral rib in the shell wall and a ventral horn outside the shell ; **D** forms a dorsal rib in the shell wall and a foot outside the shell ; two **L** form two lateral ribs in the shell wall and two feet outside the shell. **A′** was defined by Sugiyama (1993) and is applied for the skeleton extending dorsally from **A** near the junction of **A** and **AL. L**-**Rd** was defined by Funakawa (1995) and applied to the part of **AL** between **L** and the junction of **AL** and **AL**-**AL** or **D**-**AL** (Funakawa, 1995, Figure 5). A segmentation such as cephalis, thorax, abdomen and post-abdominal segments is generally used in Nassellaria. Because some plagiacanthids have no or indistinct collar stricture (Funakawa, 1994 ; 1995), this segmentation is unsuitable for detailed descriptions in this family. Hence the segmental concept follows Funakawa (1994). First segment is distinguished from second segment by one to three pairs of connecting arches and some branches of internal spicules (Figure 4).

Taxonomic descriptions

Order Polycystina Ehrenberg, 1838,
emend. Riedel, 1967
Suborder Nassellaria Ehrenberg, 1875
Family Plagiacanthidae Hertwing, 1879, emend.
Petrushevskaya, 1971a
Subfamily Clathromitrinae Petrushevskaya, 1971b

Remarks.—Sugiyama (1994) included this subfamily in the family Sethophormidae Haeckel, 1881. An emended diagnosis of Sethophormidae presented by Sugiyama (1994) is that **A, D** and two **L** have one verticil of three branches without exception. Most species of this subfamily have these branches, however, some species described in this paper lack some of the branches. Therefore the author uses this subfamily provisionally for the following three genera in the sense of Petrushevskaya (1971a). More examinations of internal and external skeletal structure are needed to establish the taxonomy of family- or subfamily-level.

Genus ***Corythomelissa*** Campbell, 1951, sensu Petrushevskaya, 1975

Type species.—*Lithomelissa corythium* Ehrenberg, 1873.

Remarks.—Composition of internal skeletal structure is as described by Funakawa (1994) except for arches located on dorsal side of shell. **A** and **V** form apical and ventral horns outside the shell wall respectively, and never lie in shell wall as apical or ventral ribs. **D** and two **L** are well developed as lateral and dorsal ribs in shell wall of second segment and prolong to become three feet outside the shell. **L**-**R** by Sugiyama (1993) is absent. Length of **L**-**Rd** is variable. Junction of **A** and **AL** is located inside the shell wall. **D** has a pair of branches which connect usually to right and left **D**-**AL** respectively when **D**-**AL** is present. **L** has a pair of indistinct branches which usually connect to **VL** and **D**-**AL** respectively. This genus has complicated internal skeletal structure and the fine internal skeletal structures are hard to reflect the external morphology.

The Late Miocene species, *Corythomelissa* sp. (*C. horrida* by Funakawa, 1994) has one **AL**-**AL** on dorsal side of shell but three species described below from the Upper Oligocene to the Lower Miocene have two **D**-**AL** instead of one **AL**-**AL**. In this paper, these four species that have different internal skeletal structures are included in the genus *Corythomelissa* because they are related phylogenetically to each other, as described in the discussion. Although the external morphology of this genus resembles several genera of Paleogene Clathromitrinae (e. g. *Spongomelissa* and *Tripodiscium*), phylogenetic relations between them are unclear because the internal skeletal structures of most species of Paleogene Clathromitrinae have not been clarified sufficiently. A schematic illustration of internal skeletal structure of the following three species is shown in Figure 4.

Corythomelissa omoprominentia sp. nov.

Figures 5-1a—2b

Type specimens.—Holotype, OCUCR-0035 : Paratype, OCUCR-0036.

Description.—Shell is composed of two segments. First segment is subspherical with an apical horn. Apical horn is three-bladed, approximately equal in length to height of first segment. External surface of first segment is thorny. Pores in first segment are circular to subcircular and irregularly distributed. In some specimens, both **D**-**AL** and **VL** are indistinct and incomplete (Figure 5-1b). Strictures between two segments are indistinct because of a thickened shell wall with numerous thorns. Ventral horn is three-bladed, extends laterally and is shorter than apical horn. **L**-**Rd** is long. Two branches arise from **D** and connect to dorsal side end of **D**-**AL**. Two branches arise from **L** ; ventral one connects to **VL** and dorsal one, usually indistinct, to **AL** or **D**-**AL**. **D**-**AL** diverges from **AL** where **AL** separates from internal surface of shell wall. **A′** is present in most specimens and diverges from **A** at a higher horizon than the junction of **A** and **AL** (Figures 5-1c, -2b). Most internal spicules are circular in section except for their external parts, such as horns and feet. Axial projections are distinct as some downwardly directed appendages. Second segment is oblate spherical at side view and subdivided into upper and lower parts by a distinct shoulder. The upper part has distinct lateral and dorsal ribs. External surface of second segment is thorny. Three feet are three-bladed and approximately equal in length to apical horn, extending obliquely downward at the shoulder of second segment. Pores in second segment are circular to subcircular and irregularly distributed. Distal aperture of second segment is sometimes closed by porous plate.

Dimensions (in μm).—Measurements are based on 14 mature specimens. Length of apical horn, 49-60 (aver-

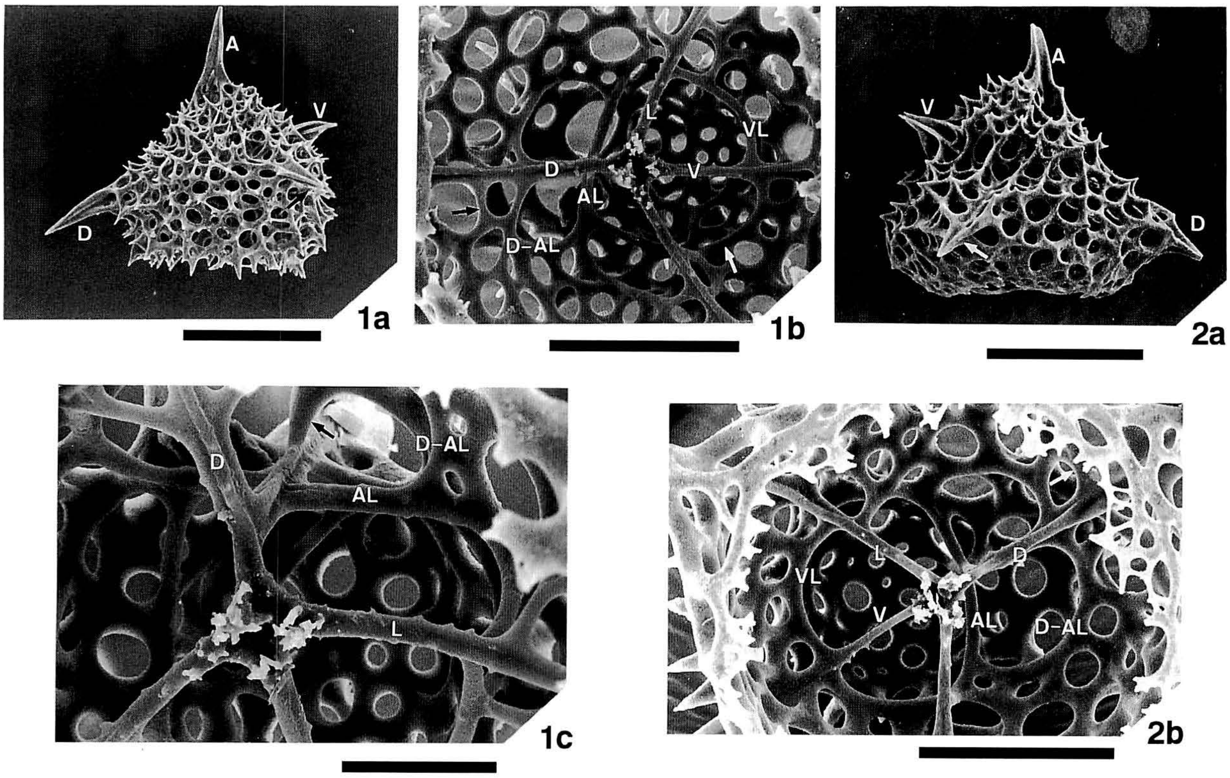

Figure 5. **1a**-**2b** : *Corythomelissa omoprominentia* Funakawa sp. nov. **1a**-**c** : OCUCR-36, MW-125, paratype. **1a** : Right lateral view ; Black arrow points to right **L**. **1b** : Basal view ; White arrow points to indistinct left **L**, black one to left branch of **D**. **1c** : Enlargement of basal view ; Black arrow points to **A′** ? **2a**-**b** : OCUCR-35, MW-125, holotype. **2a** : Left lateral view ; White arrow points to left **L**. **2b** : Basal view ; White arrow points to a dorsal branch of left **L**. Scale bars : **1a** and **2a**=100 μm ; **1b** and **2b**=50 μm ; **1c**=20 μm.

age is 53): Length of ventral horn, 27-48 (37). Outside diameter of first segment (not including ventral horn), 57-93 (72): Outside diameter of second segment (not including feet), 128-160 (143). Inside width between two **AL**, 51-70 (59): Inside depth between ends of **D** and **V**, 63-90 (72). Height of first segment (not including apical horn), 38-53 (47). Total height of shell (not including feet and apical horn), 90-139 (120).

Remarks.—This species is distinguished from *Corythomelissa horrida* Petrushevskaya by a distinct shoulder on second segment. This species is distinguished from *Euscenarium* sp. aff. *E. tricolpium* of Funakawa (1994) by the presence of two **D**-**AL** and a distinct shoulder on second segment.

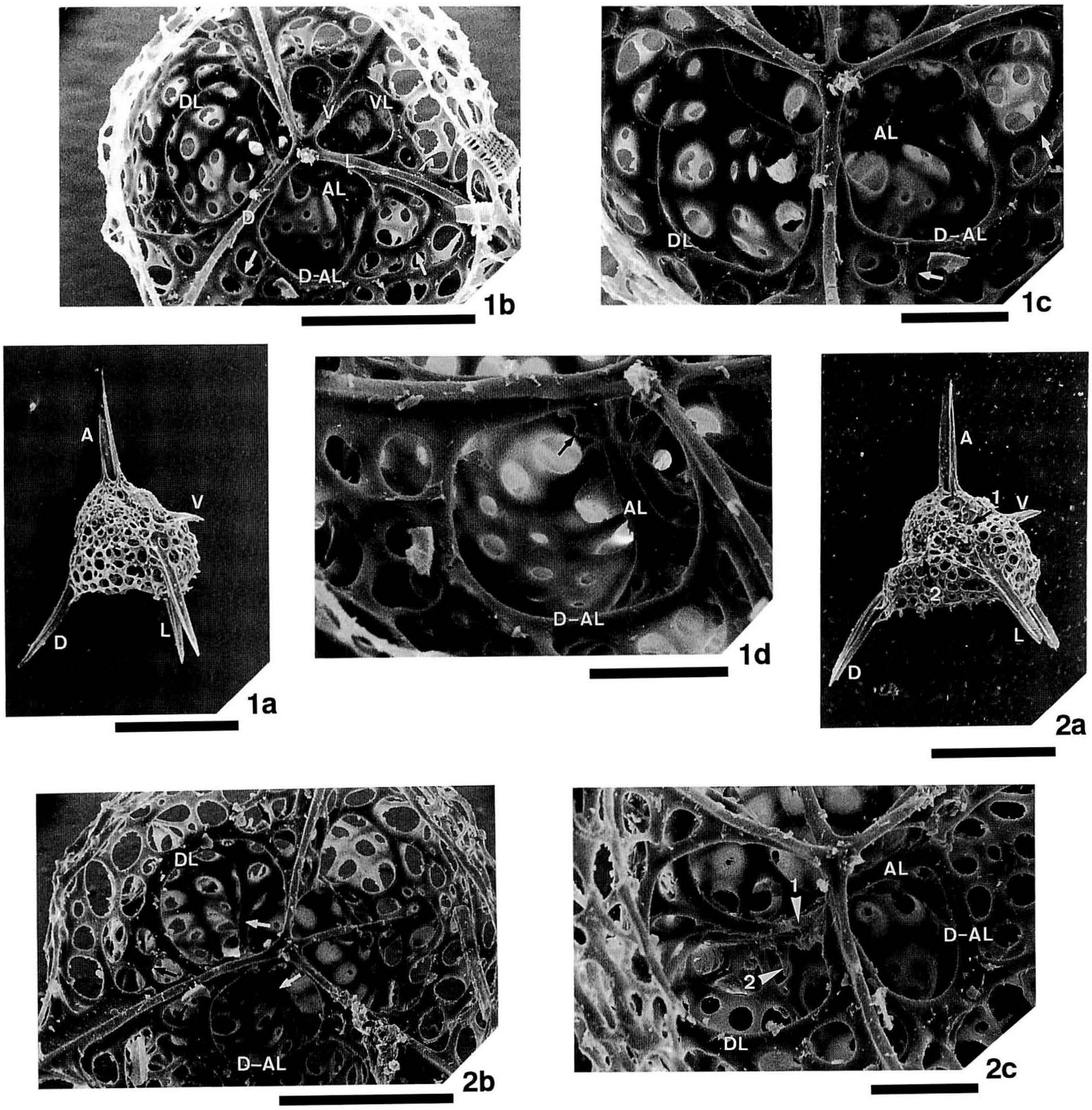

Figure 6. **1a**-**2c**: *Corythomelissa pachyostraca* Funakawa sp. nov. **1a**-**c**: OCUCR-37, 90081306, holotype. **1a**: Right lateral view. **1b**: Basal view; White arrows point to left branch of **D** and dorsal branch of left **L**. **1c**: Enlargement of basal view; White arrow points to left branch of **D**. **1d**: Enlargement of basal view; Black arrow points to **A′**. **2a**-**c**: OCUCR-38, 90081306, paratype. **2a**: Right lateral view; Arrow **1** points to the stricture along right **AL, 2** to the stricture along right **DL**. **2b**: Basal view; White arrows point to right and left **AL**, black ones to right and left branches of **D**. **2c**: Enlargement of basal view; Arrow **1** points to **A** and **2** to **A′**. Scale bars: **1a** and **2a**=100 μm; **1b** and **2b**=50 μm; **1c, 1d** and **2c**=20 μm.

Etymology.—The specific name means "distinct shoulder" in Latin.

Occurrences.—MW-125, -120 and -118. Rare to few.

Stratigraphic notes.—Lower Miocene.

Corythomelissa pachyostraca sp. nov.

Figures 6-1a—2c

Type specimen.—Holotype, OCUCR-0037 : Paratype, OCUCR-38.

Description.—Shell is composed of two segments. External surface of shell is spineless. First segment is subspherical with an apical horn. Apical horn is robust, three-bladed and twice to three times as long as height of first segment. First segment of some specimens has a thickened shell wall with very few and small pores. Pores in first segment are circular to subcircular, very small in size and irregularly distributed. Strictures along **AL** and **D-AL** are indistinct in some specimens. Ventral horn is three-bladed and much shorter than apical horn, extending laterally to obliquely upward. Length of **L-Rd** is variable but is usually very short. In most specimens, right and left **L-Rd** show different lengths. Some specimens have right or left **DL** instead of **D-AL** and **L-Rd** is absent in this case (Figures 6-1c, -2b). Two branches arise from **D** and connect to dorsal side end of **D-AL**. Two branches arise from **L** ; ventral one connects to **VL** and dorsal one, sometimes indistinct, to **AL** or **D-AL**. **D-AL** diverges from **AL** where **AL** meets the internal surface of shell wall. **A′** is distinct and spiny. Two **L** and **D** are three-bladed in section for most part. **MB**, basal part of **V** and lower part of **A** are circular in section. Axial projection is distinct. Second segment is hemispherical with three lateral and dorsal ribs. Three feet are three-bladed and approximately equal in length to apical horn. Feet extend obliquely downward from the lower part of second segment. Pores in second segment are circular to subcircular, larger than those in first segment and irregularly distributed. Distal aperture of second segment is fully open without teeth.

Dimensions (in μm).—Measurements are based on 62 mature specimens. Length of apical horn, 51-123 (84) : Length of ventral horn, 24-67 (40). Outside diameter of first segment (not including ventral horn), 58-117 (79) : Outside diameter of second segment (not including feet), 83-160 (123). Inside width between two **AL**, 46-83 (63) : Inside depth between ends of **D** and **V**, 45-93 (69). Height of first segment (not including apical horn), 30-63 (46). Total height of shell (not including feet and apical horn), 62-147 (105).

Remarks.—The variable length of **L-Rd** and the presence of one **DL** instead of **D-AL** in some specimens are considered intraspecific variation in this species because it seems that the length of **L-Rd** changes gradually. This species is distinguished from *Corythomelissa horrida* Petrushevskaya and *C. omoprominentia* sp. nov. by short **L-Rd** and a first segment with a spineless and thickened shell wall. This species is distinguished from *Euscenarium* sp. aff. *E. tricolpium* of Funakawa (1994) by the presence of **L-Rd.**

Etymology.—The specific name means "thick shell" in Latin.

Occurrences.—90081302, 90081501, 90081306 and 90081402. Few to common (90081306 and 90081402) to very rare (90081302 and 90081501).

Stratigraphic notes.—Upper Oligocene.

Corythomelissa spinosa sp. nov.

Figures 7-1a—3c

Type specimen.—Holotype, OCUCR-0039 : Paratype, OCUCR-0040, -0041.

Description.—Shell is composed of two segments. First segment is subspherical with an apical horn. Apical horn is stout, three-bladed and twice to three times as long as height of first segment. Surface of first segment is thorny. Pores in first segment are small, circular to subcircular and irregularly distributed. Ventral horn is three-bladed and shorter than apical horn, extending laterally to obliquely upward. In some specimens, **D-AL** is indistinct (Figure 7-2b). Strictures between two segments are indistinct because of the thickened shell wall with numerous thorns. **L-Rd** is long. Two branches arise from **D** and connect to dorsal end of **D-AL.** Two branches arise from each **L** ; ventral one connects to **VL** and dorsal one, usually indistinct, to **AL** or **D-AL. D-AL** diverges from **AL** where **AL** separates from internal surface of shell wall. **A′** is present in most specimens and diverges from **A** at a higher horizon than the junction of **A** and **AL** (Figure 7-1b). Most internal spicules are circular in section except for their external prolongations, such as horns and feet. Axial projections are distinct as numerous fine appendages. Second segment is hemispherical. The upper part of second segment has distinct lateral and dorsal ribs and its external surface is somewhat spiny. Three feet are three-bladed and their lengths are approxi-

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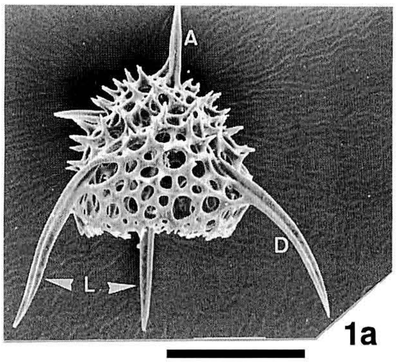
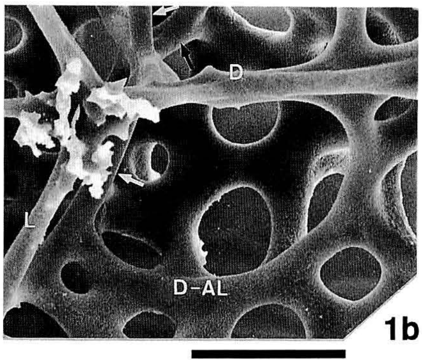
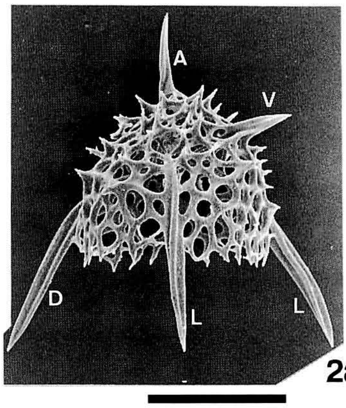
Figure 7. **1a-3c** : *Corythomelissa spinosa* Funakawa sp. nov. **1a-b** : OCUCR-39, MW-125, holotype. **1a** : Left lateral view. **1b** : Enlargement of basal view ; White arrow points to left **AL**, black one to **A′** ?. **2a-2c** : OCUCR-40, MW-125, paratype. **2a** : Right lateral to ventral view. **2b** : Basal view. **2c** : Enlargement of basal view. **3a-c** : OCUCR-41, 90081501, paratype. **3a** : Right lateral view. **3b** : Basal view ; Arrows **1** point to right and left **D-AL, 2** to right and left **AL, 3** to right **VL**, white one to right branch of **D. 3c** : Enlargement of basal view ; White arrow points to **A. 4a-4c** : *Corythomelissa* sp., Oik-7 (Modified from Funakawa, 1994). **4a** : Dorsal view. **4b** : Basal view ; Arrow **1** point to right and left **AL, 2** to **AL-AL, 3** to right and left branches of **D. 4c** : Enlargement of basal view ; White arrow points to **AL-AL.** Scale bars : **1a, 2a** and **3a**=100 μm ; **2b, 3b, 4a** and **4b**=50 μm ; **1b, 2c** and **3c**=20 μm ; **4c**=10 μm.



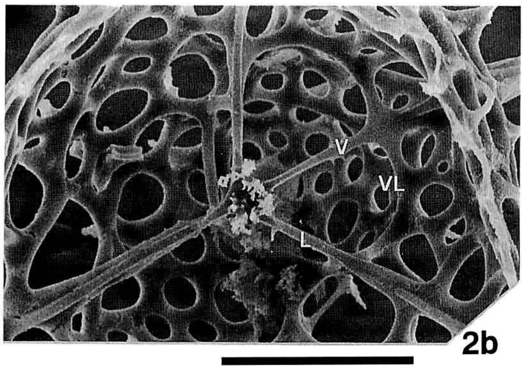
1a



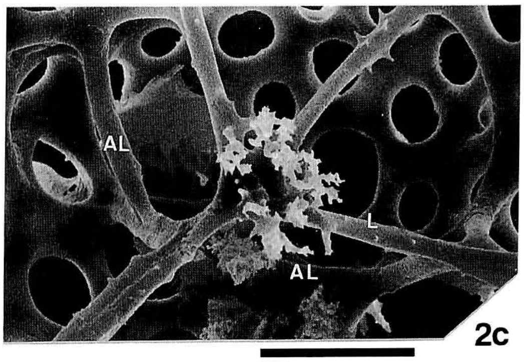
1b



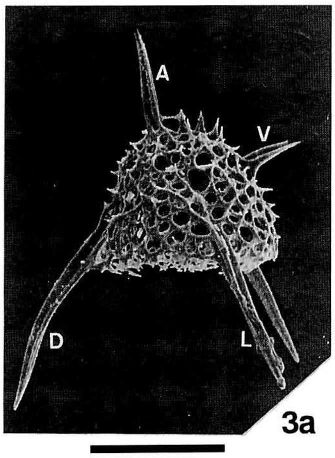
2a



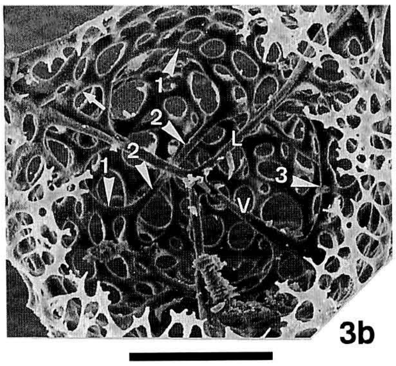
2b



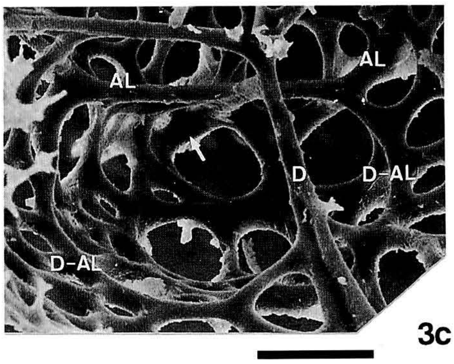
2c



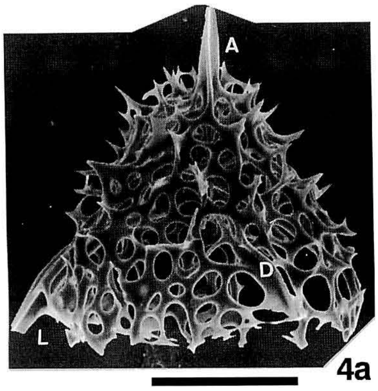
3a



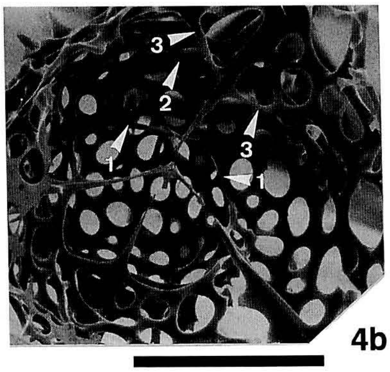
3b



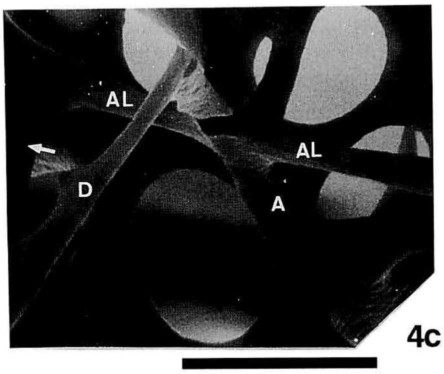
3c



4a



4b



4c

mately equal to that of apical horn. They extend obliquely downward from middle to lower part of second segment. Pores in second segment are circular to subcircular, larger than those of first segment and irregularly distributed. Distal aperture of second segment is fully open without teeth.

Dimensions (in μm).—Measurements are based on 62 mature specimens. Length of apical horn, 51-123 (84): Length of ventral horn, 24-67 (40). Outside diameter of first segment (not including ventral horn), 58-117 (79): Outside diameter of second segment (not including feet), 83-160 (123). Inside width between two **AL**, 46-83 (63): Inside depth between ends of **D** and **V**, 45-93 (69). Height of first segment (not including apical horn), 30-63 (46). Total height of shell (not including feet and apical horn), 62-147 (105).

Remarks.—This species is distinguished from *C. pachyostraca* sp. nov. by the thorny wall of first segment. This species resembles *C. horrida* but is distinguished from it by the presence of **D**-**AL** on the dorsal side of the shell. This species is distinguished from *C. omoprominentia* sp. nov. by the well developed feet and the open distal aperture of the second segment.

Etymology.—The specific name means "spinose" in Latin.

Occurrences.—All samples examined. Few in 90081302 and 90081501, very rare in 90081306 and 90081402 and common in MW-125, -120 and -118. Rare to very rare in Upper Miocene samples, Ny-89, Ny-81, 91092604 and 91092607 (Funakawa, 1993; 1994).

Stratigraphic notes.—Upper Oligocene to Upper Miocene.

Corythomelissa sp.

Figures 7-4a—c

Corythomelissa horrida Petrushevskaya: Funakawa, 1994, p. 476, figs. 14, 1a-b.

Remarks.—Shell is composed of two segments. First segment is hemispherical or cup-shaped, with an apical horn. Apical horn is stout, three-bladed and is approximately equal in length to height of first segment. Surface of first segment is thorny. Pores in first segment are circular to subcircular and are irregularly distributed. Ventral horn is three-bladed and is shorter and narrower than apical horn, extending laterally to obliquely upward. **AL**-**AL** is indistinct (Figure 7-4b). Strictures between two segments are indistinct because of the thickened shell wall with numerous thorns. **L**-**Rd** is very long. Two branches arise from **D** and connect to shell wall. Two branches arise from each **L**: ventral one connects to **VL** and dorsal one, usually indistinct, to **AL**. Two branches, sometimes indistinct, arise from **V** and connect to **VL**. **AL**-**AL** diverges from **AL** where **AL** separates from internal surface of shell wall. **A′** is absent (Figure 7-4b). Most internal spicules are circular in section except for their external prolongations, such as horns and feet. Axial projection is present. Second segment is cup-shaped. Three feet are three-bladed and their lengths are approximately equal to that of apical horn. They extend obliquely downward from middle to lower part of second segment. Pores in second segment are circular to subcircular and are irregularly distributed. Distal aperture of second segment is fully open in most specimens but in some specimens it tends to be closed by a porous plate.

Although all specimens examined in this study are *Corythomelissa horrida* Petrushevskaya of Funakawa (1994), it is questionable to identify this species as *C. horrida* because of the different ranges between *C. horrida* and Funakawa's (1994) species. *C. horrida* was described by Petrushevskaya (1975) from Antarctic Oligocene to Miocene deposits. The species was then reported by several authors: by Goll and Bjørklund (1989) from the Middle to Upper Miocene (Norwegian Sea, ODP Leg 104); and by Takemura (1992) from the uppermost Eocene to Upper Oligocene (southern Indian Ocean, ODP Leg 120). On the other hand, Funakawa's (1994) species does not occur from either the Upper Oligocene or Lower Miocene in this study. This fact indicates that Funakawa's (1994) species is different from *C. horrida*. Therefore, the author renounces Funakawa's (1994) specific identification of this species and emends it as *Corythomelissa* sp.

Dimensions and *Occurrences*.—Refer to Funakawa, 1994, p. 477.

Genus ***Euscenarium*** Haeckel, 1887, sensu Petrushevskaya, 1981

Type species.—*Euscenium tricolpium* Haeckel, 1887.

Remarks.—Composition of internal skeletal structure is as described by Funakawa (1994). **A** and **V** form apical and ventral horns outside the shell wall respectively, and never lie in shell wall as apical or ventral ribs. **D** and two **L** are well developed as lateral and dorsal ribs in shell wall of second segment and prolong to three feet outside the shell. **L**-**R** of Sugiyama (1993) and **L**-**Rd** are absent. **D** has a pair of branches which connect to right and left **DL** respectively. **L** has a pair of branches which connect to **VL** and **DL** respectively. This genus is distinguished from *Corythomelissa* by the absence of **L**-**Rd.** A schematic illustration of internal skeletal structure of the following species is shown in Figure 8.

Euscenarium microcapitalium sp. nov.

Figures 10-1a—2b

Type specimen.—Holotype, OCUCR-0042: Paratype, OCUCR-0043.

Description.—Shell is composed of two segments. First segment is hemispherical. Apical horn is three-bladed and length is equal to twice the height of first segment. Ventral horn is three-bladed and shorter than apical horn. Shell wall of first segment is thickened and usually poreless, with smooth surface. When pores are present, they are very small, circular and irregularly dis-

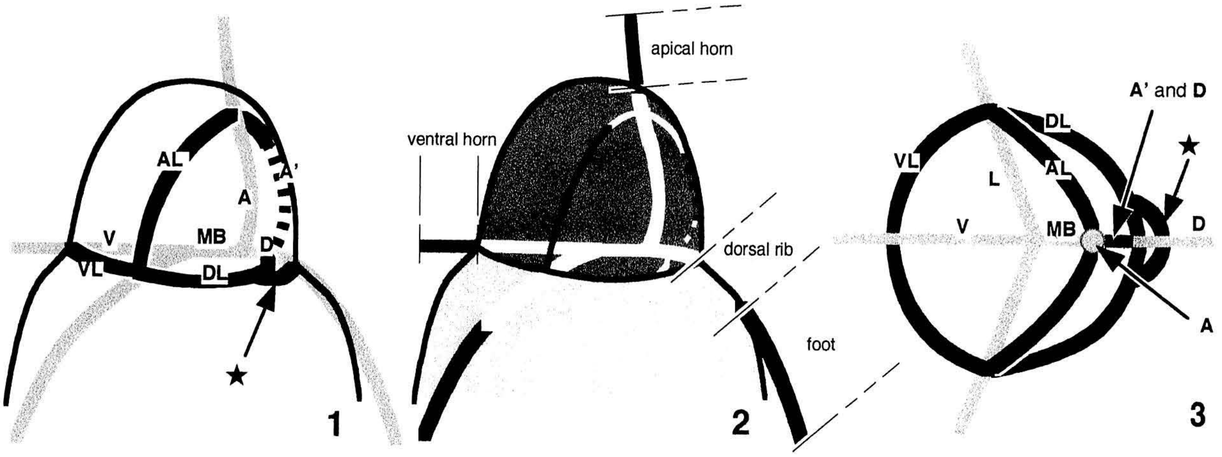


Figure 8. Diagrams of internal skeletal structure of *Euscenarium microcapitalium* Funakawa sp. nov. **1** : Internal skeletal structure of left lateral view. **2** : Subdivision of two segments with internal skeletal structure. **3** : Internal skeletal structure of apical view. Dotted lines are indistinct elements. Stars are the branches of **D** and **L**, and other abbreviations are explained in the text.

1 and **3** : Grey lines show internal spicules and black lines do connecting arches ; dotted line is indistinct element. **2** : Thick lines show internal spicules (white) and their prolongations in and outside the shell wall (black). Weak lines show connecting arches inside the shell wall (white) and in the shell wall (black). Broken line shows outline of shell. Dark grey part indicates the first segment and light grey part the second segment.

tributed. Strictures along **AL, VL** and **DL** are shallow. Junction of **A** and **AL** is inside the shell, just below the internal surface of shell. **A′** is well developed and goes down along shell wall and forms indistinct **AD.** Right and left branches arise from **D** and connect to **DL.** Ventral and dorsal branches arise from **L** and are indistinct. Most internal spicules are circular in section except for their external prolongations, such as horns and feet. Axial projection is distinct. Some specimens have one to two projections on underside of both **D** and **L.** Second segment is oblate spherical to subcylindrical with three distinct lateral and dorsal ribs. Three feet are long, three-bladed, and extend obliquely downward. Pores in second segment are circular to subcircular and larger than those of first segment. Distal aperture of second segment is fully open, without teeth.

Dimensions (in μm).—*Measurements* are based on eight mature specimens. Length of apical horn, 31-48 (40) : Length of ventral horn, 12 (measured on only one specimen). Outside diameter of first segment (not including ventral horn), 41-48 (43) : Outside diameter of second segment (not including feet), 52-64 (57). Inside width between two **DL** or **AL**, 36-43 (39) : Inside depth between ends of **D** and **V**, 37-45 (40). Height of first segment (not including apical horn), 25-32 (29). Total height of shell (not including apical horn and feet), 41-63 (51).

Remarks.—This species is smaller than *Euscenarium tricolpium* (Haeckel) and *E. joergenseni* Dumitrica. It is distinguished from *E.* sp. cf. *E. tricolpium* of Funakawa (1994) by a small first segment and shallow strictures between the two segments. This species has similar skeletal structures to *Corythomelissa pachyostraca* sp. nov. except for the smaller shell and the absence of **L**-**Rd.**

Etymology.—The specific name means "small cephalis" in Latin.

Occurrences.—Rare in 90081302, 90081501 and 90081306.

Stratigraphic notes.—Upper Oligocene.

Genus ***Lithomelissa*** Ehrenberg, 1847, sensu Petrushevskaya, 1971b

Type species.—*Lithomelissa microptera* Ehrenberg, 1854.

Remarks.—Various forms of Clathromitrinae and, perhaps Lophophaeninae, have been placed in this genus. To properly classify these forms, it is necessary to investigate their internal skeletal structure. The following species has external skeletal characteristics similar to the type species, *Lithomelissa microptera* Ehrenberg, therefore it is provisionally assigned to *Lithomelissa* in this paper. A schematic illustration of the internal skeletal structure of the following species is shown in Figure 9.

Lithomelissa trifoliolata sp. nov.

Figures 10-3a—4c

Clathrolychnus sp Sugiyama, 1994, pl. 2, fig. 3a-b.

Type specimens.—Holotype, OCUCR-0044 : Paratype, OCUCR-0045.

Description.—Shell is composed of two segments. Internal skeletal structure is composed of **MB, A, D, V,** two **L**, two **AL**, two **DL**, two **VL**, **LL** and **AD (A′). L**-**R** and **L**-

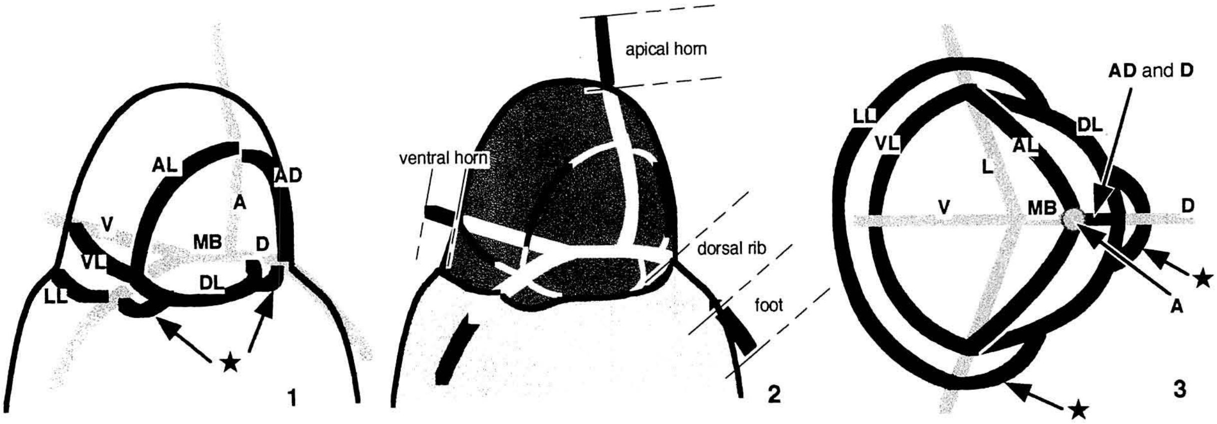


Figure 9. Diagrams of internal skeletal structure of *Lithomelissa trifoliolata* Funakawa sp. nov. **1**: Internal skeletal structure of left lateral view. **2**: Subdivision of two segments with internal skeletal structure. **3**: Internal skeletal structure of apical view. Stars are the branches of **D** and **L** and other abbreviations are explained in the text.

1 and **3**: Grey lines show internal spicules and black lines connecting arches; dotted line is indistinct element. **2**: Thick lines show internal spicules (white) and their prolongations in and outside the shell wall (black). Weak lines show connecting arches inside the shell wall (white) and in the shell wall (black). Broken line shows outline of shell. Dark grey part indicates the first segment and light grey part the second segment.

Rd are absent. At the ventral side of shell, there is one **LL** below two **VL**. **A** forms an apical horn but does not form an apical rib in shell wall of first segment. Apical horn is stout, three-bladed and approximately equal in length to height of first segment. Apical horn has lateral projections extending from three blades, which sometimes become narrow strings that connect to external surface of first segment. **V** forms a very fine ventral horn. First segment is hemispherical and distinguished from second segment by strictures along **DL**, **LL** and some branches of **L** and **D**. Junction of **A**, **A′** and **AL** is inside the shell. **A′** is well developed and forms **AD**. Right and left branches arise from **D** and connect to right and left **DL** respectively. Ventral and dorsal branches arise from **L** and the latter connects to **DL**. Shell wall of first segment is thickened and external surface is very rough. Pores in first segment are restricted to its basal part and are circular to subcircular. Most internal spicules are circular in section except for their external parts, such as horns and feet. Axial projection is distinct. There are no projections on underside of either **D** or **L**. Second segment is irregularly cylindrical. Lateral and dorsal ribs are difficult to distinguish from complex meshwork on external surface of second segment. The three feet are three-bladed and shorter than apical horn. Pores in second segment are irregularly shaped, variable in size and irregularly distributed. Distal aperture of shell is fully open, without teeth.

Dimensions (in μm).—Measurements are based on nine mature specimens. Length of apical horn, 47-65 (57). Outside diameter of first segment, 66-83 (77): Outside diameter of second segment (not including feet), 79-139 (110). Inside width between two **DL**, 49-68 (58): Inside depth between ends of **D** and **V**, 54-71 (62). Height of first segment (not including apical spine), 52-71 (63). Total height of shell (not including spical spine and feet), 110-159 (136).

Remarks.—The internal skeletal composition of this species is very similar to that of *Euscenarium microcapitalium* sp. nov. but is distinguished by well developed **A′** which forms distinct **AD**. This species is distinguished externally from *Euscenarium microcapitalium* by an irregularly cylindrical second segment and poorly developed feet. The internal skeletal structure resembles that of *Corythomelissa pachyostraca* sp. nov. but is distinguished from it by the presence of **AD** and the adsence of **L**-**Rd**. This species resembles *Lithomelissa sphaerocephalis* Chen but is distinguished from it by a larger first segment. It is distinguished from *L. challengerae* Chen by a smaller second segment, from *L. tricornis* Chen by the number of horns extending from the surface of the first segment and from *L. robusta* Chen by a smaller shell (Chen, 1975).

Etymology.—The specific name means "with three blades" in Latin.

Occurrences.—Very rare in 90081501 and few in 90081306.

Stratigraphic notes.—Upper Oligocene in eastern Hokkaido. Sugiyama (1994) reported this species from the Lower Miocene Toyohama Formation, Morozaki Group, in central Japan.

Temporal change of internal skeletal structure in *Corythomelissa*

Four species of *Corythomellissa* have characteristic connecting arch compositions. *C. pachyostraca* is char-

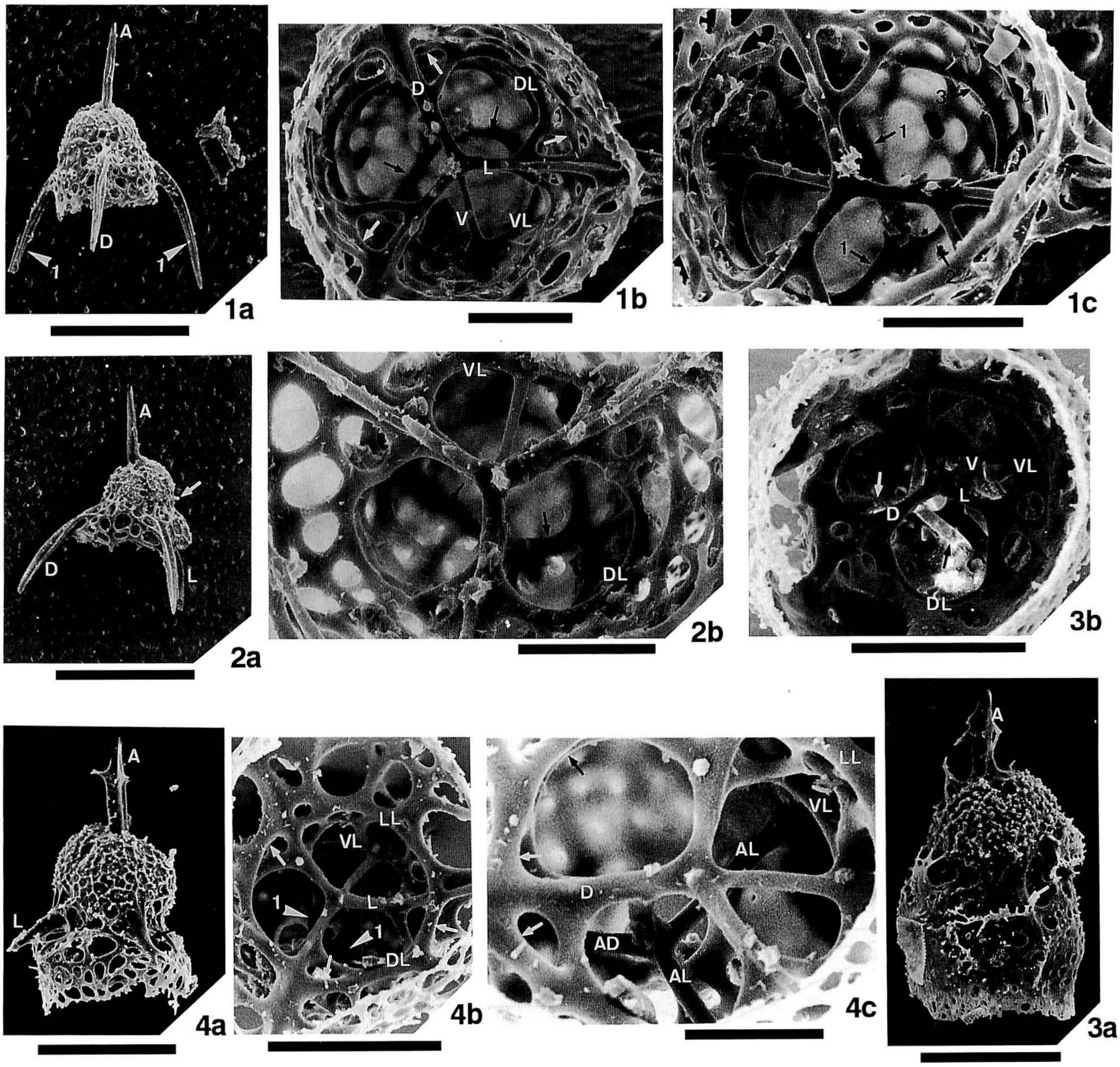


Figure 10. **1a**-**2b** : *Euscenarium microcapitalium* Funakawa sp. nov. **1a**-**c** : OCUCR-42, 90081306, holotype. **1a** : Dorsal view ; White arrows point to right and left **L**. **1b** : Basal view ; White arrows point to right branch of **D** and dorsal branch of left **L**, black ones to right and left **AL**. **1c** : Enlargement of basal view ; Arrows **1** point to right and left **AL**, **2** to **A′** and **3** to left **DL**. **2a**-**b** : OCUCR-43, 90081306, paratype. **2a** : Right lateral view ; White arrow of **2a** points to **V**. **2b** : Basal view ; Black arrows point to right and left **AL**. **3a**-**4c** : *Lithomelissa trifoliolata* Funakawa sp. nov. **3a**-**b** : OCUCR-44, 90081306, holotype. **31** : Right lateral view ; White arrow points to right **L**. **3b** : Basal view ; Black arrows point to right and left **AL**, white one to **AD** (**A′**). **4a**-**c** : OCUCR-45, 90081306, paratype. **4a** : Dorsal view ; Black arrow points to **D**. **4b** : Basal view ; White arrows point to left branch of **D** and dorsal branch of right **L**, arrows **1** to right and left **AL**. **4c** : Enlargement of basal view ; White arrows point to right and left branches of **D**, black one to right **DL**. Scale bars : **1a, 2a, 3b** and **4b**=50 μm ; **3a** and **4a**=100 μm : **1b, 1c, 2b** and **4c**=20 μm.

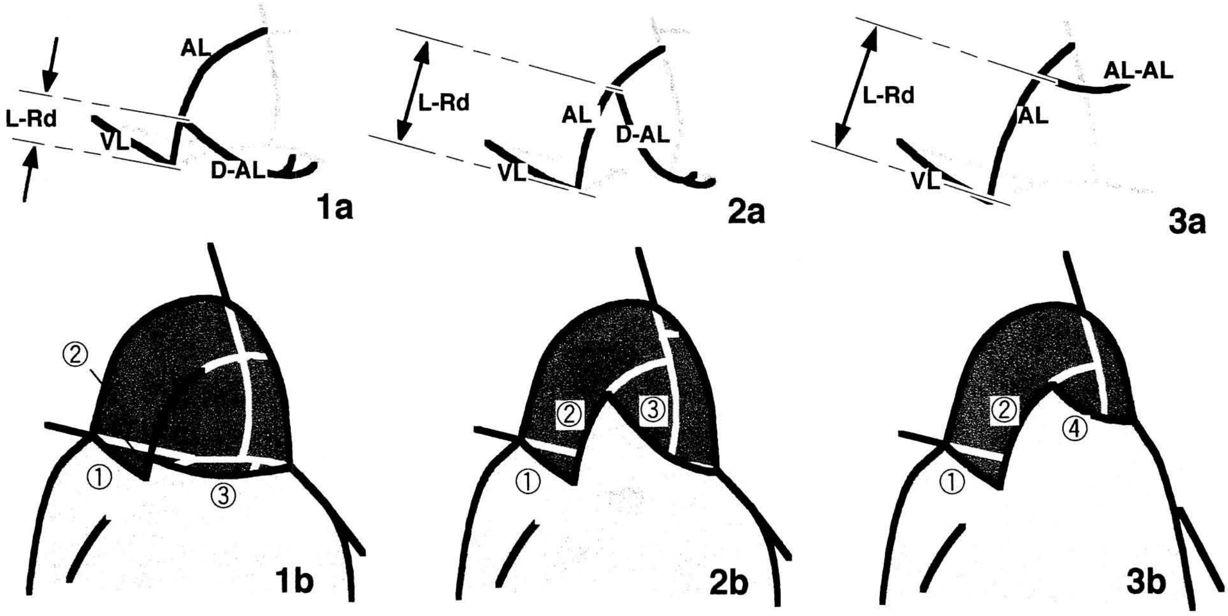


Figure 11. Temporal changes in internal skeletal structure of *Corythomelissa* from Late Oligocene to Late Miocene time. All figures are left lateral views. **1a, b** : *C. pachyostraca*. **2a, b** : *C. spinosa* and *C. omoprominentia*. **3a, b** : *C.* sp. of Funakawa. **1a, 2a, 3a** : Enlarged diagrams of internal skeletal structure, showing connecting arches as black lines and internal spicules as grey lines. **1b, 2b, 3b** : Diagrams of strictures between the first and second segments ; Dark grey part indicates the first segment and light grey part the second segment ; White lines show the elements inside the shell and black lines those in and outside the shell wall ; ①-④ show the structures in the shell surface along arches **VL** (①), **AL** (②), **D-AL** (③), and **AL-AL** (④).

Table 1. Occurrences of examined species of *Corythomelissa*, *Euscenarium* and *Lithomelissa* in this study.

Epoch	U. Oli			L. Mio	U. Mio
species / sample No.	90081302 90081501	90081306	90081402	MW-125 -120 -118	Ny -89 -81 91092607 91092601
Corythomelissa pachyostraca	+	F	F		
Corythomelissa spinosa	F	+	+	C	R
Corythomelissa omoprominentia				F	
Corythomelissa sp. of Funakawa					R
Euscenarium microcapitalium	R	R			
Lithomelissa trifoliolata	+	F			

+ : Very rare ; R : Rare ; F : Few ; C : Common.

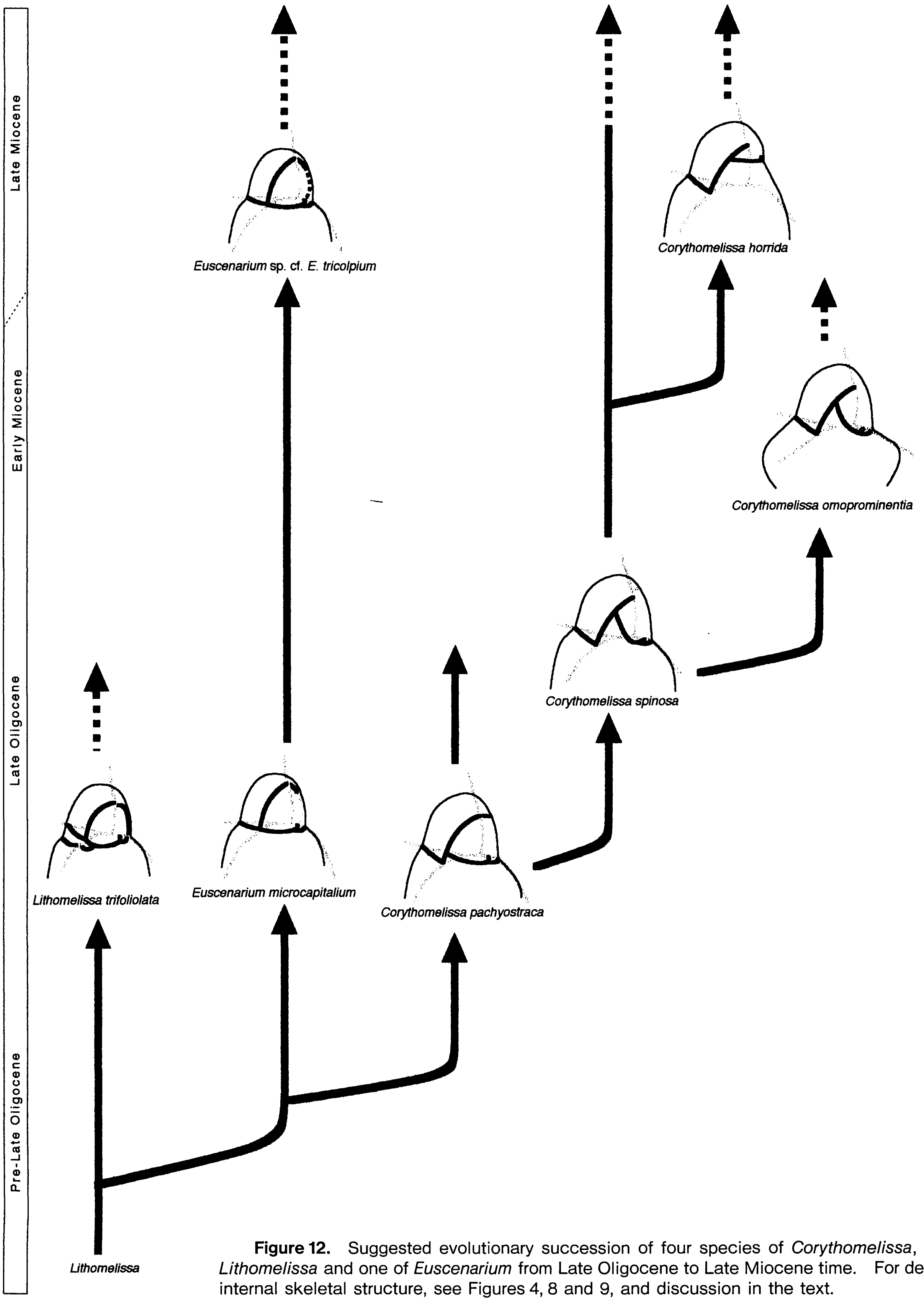


Figure 12. Suggested evolutionary succession of four species of *Corythomelissa*, one of *Lithomelissa* and one of *Euscenarium* from Late Oligocene to Late Miocene time. For details of internal skeletal structure, see Figures 4, 8 and 9, and discussion in the text.

acterized by short **L-Rd**, usually two **D-AL** and distinct **A′** (Figures 6-1d, -2c). The internal skeletal structure of this species exhibits considerable intraspecific variation; right or left **L-Rd** may be absent and at this side, **D-AL** is replaced by one **DL** (Figures 6-1c, -2c). *C. spinosa* and *C. omoprominentia* are characterized by long **L-Rd** and two **D-AL** (Figures 5-1b, -2b; 7-3c). A Late Miocene *C.* sp. of Funakawa is characterized by long **L-Rd** and one **AL-AL** (Figure 7-4b). These features are considered to be important intrageneric skeletal differences and the basic elements of the internal skeletal structure changed little from Late Oligocene to Late Miocene time: connecting arch had been transformed significantly through time (Figure 11).

Features of the occurrences of four species from the Upper Oligocene to Upper Miocene are noteworthy (Table 1); (1) *C. pachyostraca* is restricted to the Upper Oligocene and absent in the Lower to Upper Miocene, (2) *C. spinosa* is common to rare in the Upper Oligocene to Upper Miocene, (3) *C. omoprominentia* appears in the Lower Miocene, (4) *C.* sp. of Funakawa is rare in the Upper Miocene. It is considered that these patterns of occurrence reflect an evolutionary succession. On the other hand, fluctuating abundance of *C. pachyostraca* and *C. spinosa* through Late Oligocene time may represent an environmental change within the inner zone of the Kuril Arc (Fukusawa and Ishihara, 1992).

These four species exhibit three distinct trends of morphological change of internal skeletal structures from Late Oligocene to Late Miocene time (Figure 11). The first trend is an increase in length of **L-Rd**; **L-Rd** is very short in *C. pachyostraca*, generally longer in *C. spinosa* and *C. omoprominentia* and longest in *C.* sp. of Funakawa. The second trend, which is related to **L-Rd** prolongation, is a change in the arch position on the dorsal side of shell. *C. pachyostraca, C. spinosa* and *C. omoprominentia* have two **D-AL**, and these arches connect with **D**, while *C.* sp. of Funakawa has one **AL-AL** which passes above **D.** This trend indicates that the arches on the dorsal side rose in time through Early to Late Miocene. The third trend is disappearance of **A′**: *C. pachyostraca* has distinct **A′**: *C. spinosa* and *C. omoprominentia* have indistinct **A′** that diverges from **A** at a higher horizon than the junction of **A** and **AL**; *C.* sp. of Funakawa does not have **A′**. It is clear that these three trends in internal skeletal structures represent evolutionary change in these four

Table 2. Compiled occurrences of *Corythomelissa, Euscenarium* and *Lithomelissa* in previous studies.

	Eocene	Oligocene	Miocene	Pliocene	Pleistocene to Recent
Corythomelissa horrida Petrushevskaya			4, 11		5
Corythomelissa pachyostraca sp. nov.		●	●		
Corythomelissa spinosa sp. nov.			●		
Corythomelissa omoprominentia sp. nov.			●		
Corythomelissa sp.					5
Euscenarium tricolpium (Haeckel)					2
Euscenarium joergenseni (Dumitrica)			8		
Euscenarium aff. *tricolpium* (Haeckel)			11		
unnamed *Euscenarium*			11	9	
Euscenarium microcapitalium sp. nov.		●			
Lithomelissa charengerae Chen		6, 10			
Lithomelissa ehrenbergi Bütschli	1				
Lithomelissa cheni Caulet		7	3, 6, 7		
Lithomelissa duoliphysa Caulet		7			
Lithomelissa mitra Bütschli	1				
Lithomelissa sp. *L.* aff. *mitra*		3			
Lithomelissa robusta Chen		3, 6			
Lithomelissa sphaerocephalus Chen	10	6, 10			
Lithomelissa tricornis Chen	10	3, 6, 10			
Lithomelissa trifoliolata sp. nov.		●			

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● : This paper
1 : Bütschli (1882)
2 : Haeckel (1887)
3 : Chen (1975)
4 : Petrushevskaya (1975)
5 : Nishimura and Yamauchi (1984)
6 : Abelmann (1990)
7 : Caulet (1991)
8 : Sugiyama (1992)
9 : Sugiyama et al. (1992)
10 : Takemura (1992)
11 : Funakawa (1994)

species (Figure 12) : *C. spinosa* evolved from *C. pachyostraca* at Late Oligocene or pre-Late Oligocene time ; *C.* sp. of Funakawa evolved from *C. spinosa* through Early Miocene to Late Miocene time. Because *C. omoprominentia* has internal skeletal structures similar to *C. spinosa*, it is considered that *C. omoprominentia* evolved from *C. spinosa* through Late Oligocene to Early Miocene time.

Phylogeny of Late Oligocene to Miocene Clathromitrinae based on their internal skeletal structures

Corythomelissa pachyostraca has two short **L**-**Rd**, two **D**-**AL** and distinct **A′**. This internal skeletal structure is very similar to that of *Euscenarium microcapitalium* sp. nov. and *Lithomelissa trifoliolata* sp. nov., although the latter two species have two **DL** on the dorsal side and **AD**, but do not have **L**-**Rd**. If the trends of increasing length of **L**-**Rd** and decline of **A′** of *Corythomelissa* are extrapolated back in time, the internal skeletal structure of a pre-Late Oligocene form would be very similar to that of *Euscenarium microcapitalium.* Furthermore, if the decline of **A′** is extrapolated back in time, the internal skeletal structure of *E. microcapitalium* would be similar to that of *Lithomelissa trifoliolata*. These skeletal similarities suggest a provisional hypothesis : *C. pachyostraca* evolved from *E. microcapitalium* or from species ancestral to it ; *E. microcapitalium* evolved from *Lithomelissa trifoliolata* or from species ancestral to it.

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997 Upper Paleozoic bryozoans from the Lake Titicaca region, Bolivia

Part 1. Introductory remarks, stratigraphy and systematic paleontology

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Abstract. A biostratigraphic analysis of the bryozoan fauna of the Upper Paleozoic Copacabana Group in the Lake Titicaca region identified 15 genera and 45 species. Eight of the bryozoan species are new and 14 are presently not assignable to specific taxa. The new species are the cystoporates *Fistulipora carrascoi, F. titicacaensis, F. multidiaphragma*, the trepostomes *Stenodiscus altiplana, Pseudobatostomella micropora, P. yanagidai*, the cryptostome *Rhombopora kawabei* and fenestrate *Septopora andeana*. Biogeographically, among the 23 formerly described species, eight are endemic to the Andean province, seven are common to the Midcontinent province of North America and eight are found in the Tethyan province. The bryozoan faunas indicate a strong relationship with those of the Midcontinent province although considerable migration from the Tethyan realm presumably occurred.

Key words : Bryozoans, biostratigraphy, Copacabana Group, Lake Titicaca region (Bolivia), Upper Paleozoic

Introduction

The present paper, devoted to the stratigraphic and taxonomic descriptions of Upper Paleozoic bryozoans from the Lake Titicaca region, Bolivia, was originally conceived as an article to be published in the *Special Paper* series of the Palaeontological Society of Japan. Aiming for an earlier date of its publication, however, an unorthodox style of publication is adopted herein with the original article being split into two separate papers to be printed in two sequential numbers of this quarterly journal. Introductory sentences, all the stratigraphic information and the description of cystoporate and trepostome bryozoans appear in Part 1 of the paper. Part 2 will deal with the description of cryptostome and fenestrate bryozoans and the bibliographic references including all those cited in both Parts 1 and 2.

Although knowledge of Upper Paleozoic bryozoan faunas has increased, that of South America has remained poor. Bassler (1936) established a new genus, *Rhomboporella* from the "Carboniferous" in Bolivia which is now considered to be a junior synonym of *Rhombotrypella*. Chronic (in Newell, 1949, 1953) described 18 species from nine genera including 15 new species and two new genera from the Copacabana Group in Peru. Unfortunately, all his identifications were based on silicified surficial features of the bryozoan colonies.

Since 1980 I have led a team of Japanese geologists to carry out biostratigraphic field surveys of the Copacabana Group in the central Andean region in Peru and Bolivia. Some preliminary results have been reported by Sakagami (1983, 1984 *ed.*, 1986 *ed.*), Sakagami *et al.* (1981, 1983, 1985, 1991), Sakagami and Mizuno (1994), Nagai (1983) and Yanagida (1983). The present study analyzes the bryozoan fauna from the Copacabana Group in the Bolivian part of the Lake Titicaca region, where abundant fossils including bryozoans, fusulines, corals, brachiopods, molluscs and others were collected.

The Copacabana Group

1. Pevious work

The name Copacabana was used originally by Cabrera and Petersen (1936) for the upper part of the limestone section exposed at the Strait of Tiquina. Because D' Orbigny (1842) considered the brachiopods from Yaurichambi to be Carboniferous in age, the geological age of the Copacabana limestone was believed to be Carboniferous by almost all later investigators. Dunbar and Newell

(1946), however, proposed the term Copacabana Group for the entire group of Upper Paleozoic rocks of the Copacabana Peninsula and the Strait of Tiquina, and pointed out that the Copacabana Group at Yaurichambi was Early Permian (Wolfcampian) in age, based on the fusuline fauna.

In the Lake Titicaca region, Newell (1949) measured three stratigraphic sections of Upper Paleozoic sediments cropping out at Tiquina, Pirhuate and Munani. His Lower Permian Copacabana Group consisted of massive gray cherty limestone interbedded with gray and red-colored shales. The basal part of the sequence is comprised of dark gray and black shales (part of which is nonmarine in origin). Locally, the upper part had a massive, unfossiliferous red sandstone unit (Tiquina sandstone).

The comprehensive studies on Paleozoic Group of the Andean region (especially in Peru and Bolivia) by Newell (1949), and Newell, Chronic and Roberts (1949, 1953) are well known. Newell *et al.* (1953) recognized four major divisions in the Upper Paleozoic of Peru, namely in ascending order, Mississippian Ambo Group consisting of dominant sandstone with thin black shales and coal (total thickness unknown, exceeding 2,700 ft), Pennsylvanian Tarma Group consisting of thin-bedded limestones and black shales (maximum thickness about 6,900 m) and disconformable with the Ambo Group, Pennsylvanian and Permian Copacabana Group consisting of massive limestones and black shales (maximum thickness about 6,300 m), and Permian Mitu Group consisting of red beds and volcanics (maximum thickness about 12,000 ft). They measured and studied nineteen stratigraphic sections in Peru, and described many marine fossils including fusulines, brachiopods, bryozoans, molluscs and echinoderms.

Subsequently, Maeda (1977) reviewed the previous geological work, the geotectonic problems of the Copacabana Group in the Bolivian region. Urdininea and Yamagiwa (1980) recognized three fusuline subzones (namely, the *Triticites nitens, Pseudoschwagerina texana* and *Eoparafusulina gracilis* subzones) in the *Pseudoschwagerina* zone in the Copacabana Group at Cerro Jacha Khatawi in Yaurichambi.

In 1980, a group of Japanese geologists (Sakagami *et al.*, 1981, 1983) mapped the geology of the area between Lihuirco and Quisuar in the northern part of Abancáy, Peru, where the Permian Copacabana Group is well developed, and discussed the geologic structure of the area. Subsequently, Nagai (1983) discussed some of the sedimentary environments of the Copacabana Group. Numerous fossils including fusulines, bryozoans, brachiopods, molluscs and others were collected from 34 outcrops and rock samples for sedimentary petrographic study were taken from about 150 points along the route. In 1982, another biostratigraphic field survey (Sakagami *et al.*, 1984) studied the Copacabana Group developed at Cerro Jacha Khatawi in Yaurichambi and made stratigraphic sections along three routes on a small hill at Cerro Jacha Khatawi. Abundant fossils such as fusulines, bryozoans, brachiopods, molluscs and others were collected. Arellano (1983) described two new Permian species of trilobites from this region, namely *Paladin yampupatensis* from Yampupata and *Ditomopyge derimsi* from Yaurichambi. Kobayashi and Hamada (1986) studied trilobite specimens collected by Sakagami from the basal part of the Copacabana Group at Chirapaca, about 8 km north of Copacabana as shown in Figure 8. They proposed a new genus, *Bolivicrania*, designating *Paladin yampupatensis* Arellano as the type species.

In our field work of 1984 (Sakagami *et al.*, 1985; Sakagami *ed.*, 1986), stratigraphic sections were made along some routes around Lake Titicaca, namely Cuyavi, Yampupata, Ancoraimes and Matilde, where the Copacabana Group is well distributed.

Suarez-Riglos *et al.* (1987) reported on the conodont biostratigraphy of the Copacabana Group and divided it into four conodont assemblage zones, namely, *Streptognathodus elongatus, Idiognathodus ellisoni, Neogondolella bisselli-Sweetognathus whitei* and *Neostreptognathodus pequopensis-Sweetognathus behnkeni* Assemblage Zones, in ascending order. They considered the lower two assemblage zones, which were previously recognized as lowermost Permian (*Triticites* zone; *Triticites nitens* subzone) as uppermost Carboniferous (Virgilian) based on the conodont data.

Wilson (1990) described Permian corals from the Copacabana Group in Bolivia and confirmed that they belonged to the Cyathaxonid Coral Province, which is restricted to South and Central America, Mexico and the Texas-Oklahoma-Midcontinent region, USA.

Sakagami *et al.* (1991) reexamined the Copacabana Group distributed along the above-mentioned routes and collected rock samples for conodont analysis especially around the boundary between the *Triticites* and *Pseudoschwagerina* zones. Suarez-Riglos *et al.* (1987) revised the correlation of stratigraphic sections and the boundary between the Carboniferous and the Permian was placed at the base of the *Pseudoschwagerina* zone. Sakagami and Mizuno (1994) discovered fusulines (*Profusulinella*) and conodonts indicating an Atokan (early Middle Pennsylvanian) age for the lower part of the Copacabana. This was previously considered to be Virgilian (latest Pennsylvanian) to Leonardian (early Middle Permian) in age.

2. Stratigraphic sections of the Copacabana Group exposed around Lake Titicaca

The geological map (scale: 1/1,000,000) made by GEOBOL (Geological Survey of Bolivia, 1978) shows the Copacabana Group divided into two belts with a NW-SE trend diverging at Yaurichambi. One belt on the southwestern side is narrowly distributed from Yaurichambi to the northeastern slope of Cumana-Cuyavi and then to the southwestern slope of Yampupata (northwestern part of Copacabana Peninsula). Another belt on the notheastern side is in a complicatedly folded structure of Devonian, Carboniferous, Permian and Mesozoic or Tertiary strata in the northeastern part of Titicaca Lake. In addition to

Figure 1. Map showing the locations of biostratigraphic sections measured in the Copacabana Group.

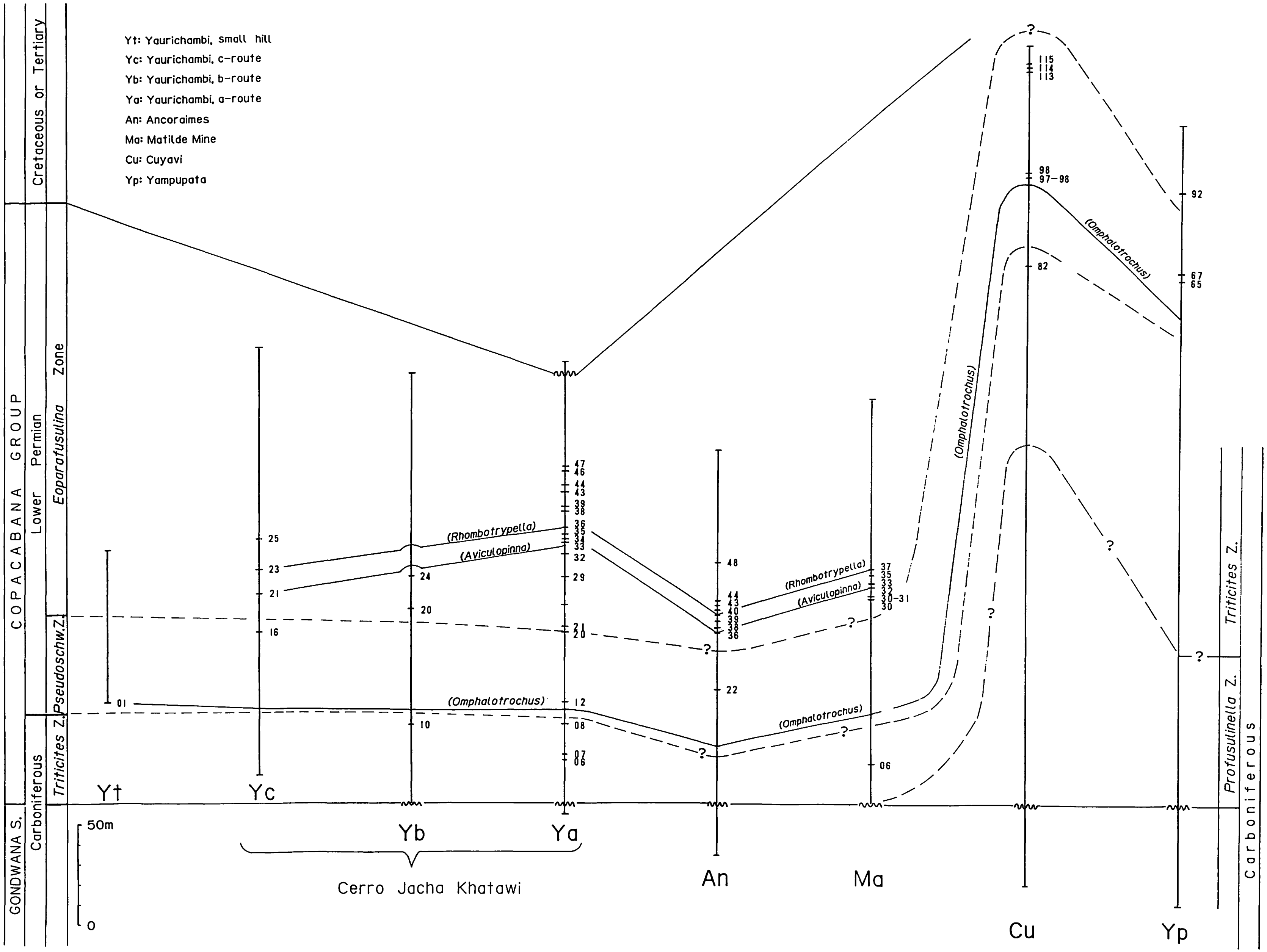


Figure 2. Correlation chart of simplified columnar sections of the Copacabana Group in the Lake Titicaca region. Numbers show horizons in which bryozoan and some other fossils occur.

Cerro Jacha Khatawi where three stratigraphic sections were made in 1982 (Sakagami *ed*., 1984), stratigraphic sections at an original scale of 1 : 100 were also made along the following five routes where the Copacabana Group is well developed, namely, small Yaurichambi hill (Yt), Cuyavi, Yampupata, Ancoraimes and Matilde routes (Figure 1).

(1) Yaurichambi

Cerro Jacha Khatawi in Yaurichambi (Figure 3) consists of a monadnock situated at about 50 km WNW of La Paz City and well known because of its abundant fossils (fusulines, brachiopods, bryozoans, gastropods, corals and others) in many stratigraphic horizons. A geological map of the hill at an original scale of 1 : 5,000 (Figure 4) and measured stratigraphic sections (Figure 2) along three routes : Ya-, Yb- and Yc-routes show where many samples were collected.

Cerro Jacha Khatawi is subdivided geomorphologically into two small hills. There are three major faults and some minor faults, which are perpendicular to the general strike of the formation. Throws of these major faults are about 10 m to 20 m. Devonian, Carboniferous, Permian and Tertiary stratigraphic units trend generally in a NW-SE direction and dip to the southwest.

The Devonian Sica Sica Series consists of alternating beds of pale gray to pale green, muscovite-bearing, fine to medium-grained sandstone and shale with well developed small-scaled crosslaminae. The series is more than 120 m thick and the lowest part is obscured. The General strike and dip are N75°W and 35°S, respectively.

The Carboniferous Gondwana Series apparently overlies unconformably the Sica Sica Series, but the relationship between these two units cannot be observed. This Gondwana Series consists mainly of pale purple sandstone. In contrast with the Sica Sica Series, it has less muscovite and greater quartz content. The cross-laminations of this series become larger in scale than those of the Sica Sica Series. The thickness is about 20 m, and the general strike and dip are N50°-60°W and 60° S-90°, respectively. The relationship between the Gondwana Group and overlying Copacabana Group is considered to be disconformable.

The Copacabana Group consists mainly of alternating beds of limestone and mudstone, with some dolostone and nodular chert. Only two layers are shown in the geological map (Figure 4). Unit Ya10 may correspond to Yb11 in Yb-route and Yc08 in Yc-route. This is confirmed by the presence of a characteristic gastropod, *Omphalotrochus*, at these three sites. It is also clear that Ya36 corresponds to Yc23 in Yc-route (but obscure in Yb-route) based on the occurrence of bryozoans including *Rhombotrypella* and a brachiopod (*Composita*) at these two sites (Figure 4). The upperrmost part of this group is intercalated with pale green or pale brown chert or cherty limestone. Among the fossils, brachiopods predominate in many horizons throughout the group ; fusulines and bryozoans are rare in the lower part but become very

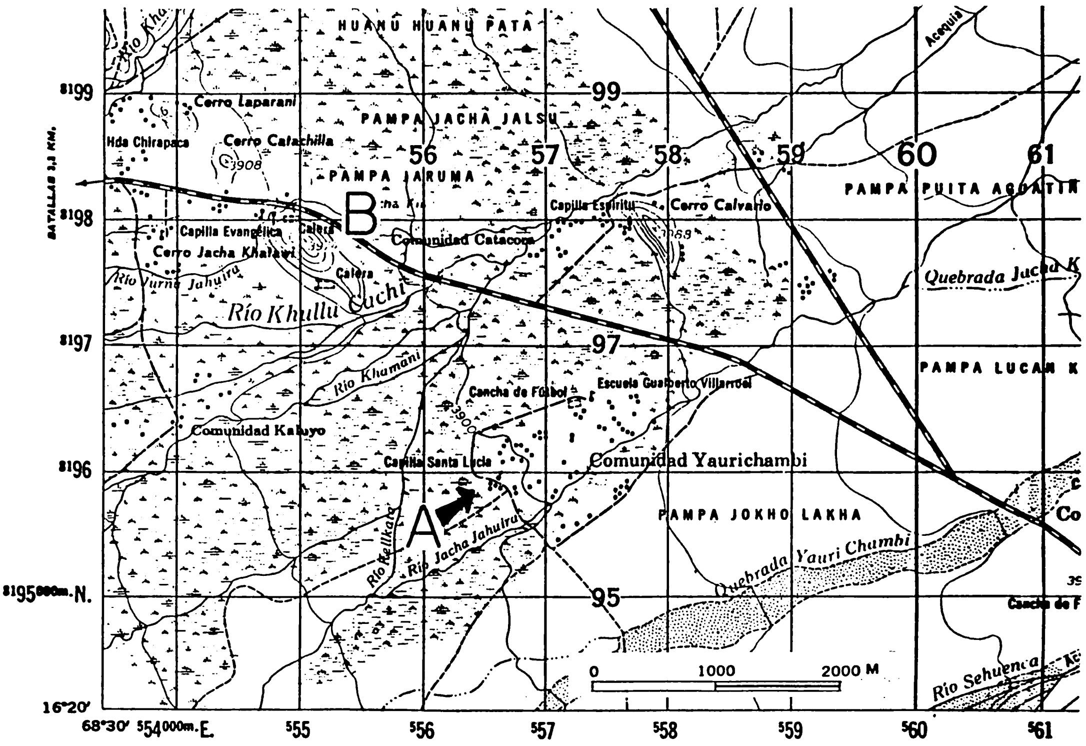


Figure 3. Topographic map showing the situation of a small hill of Yauricambi(A) and Cerro Jacha Khatawi(B) (from Carta Nacional Bolivia 1 : 50,000 "Peñas").

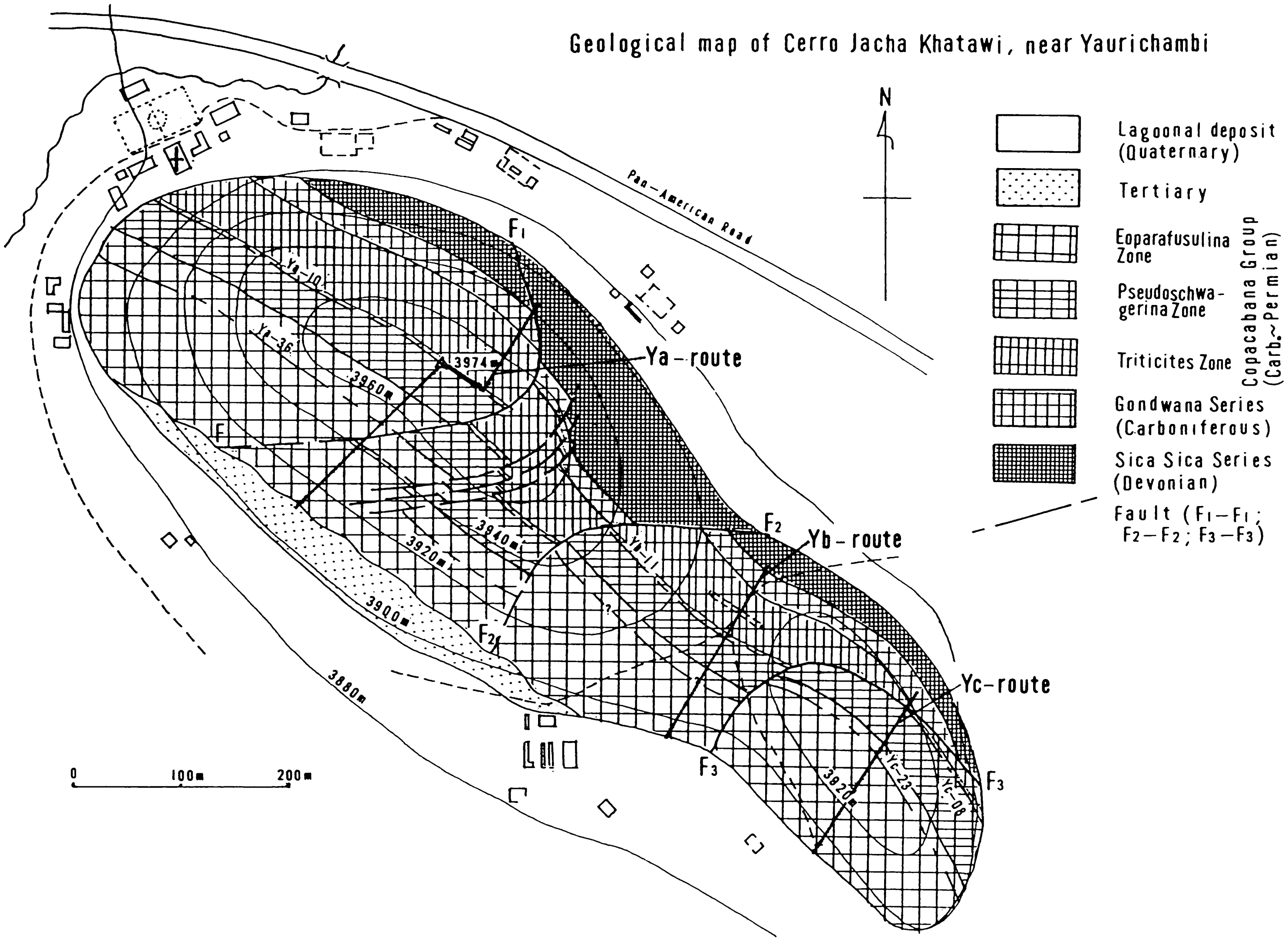


Figure 4. Geological map of Cerro Jacha Khatawi in Yaurichambi (from Sakagami *et al.*, 1991), showing the Yaurichambi (Ya, Yb and Yc) sections.

numerous in the upper part; and corals, gastropods, and bivalves are rare but crowded together in some horizons. A bivalve, *Aviculopinna*, is predominant in Ya33 and Yc21, and these two localities are considered to be at the same horizon.

Numerous "Lebensspuren"-like materials are present in many horizons of the upper half of this group. Most of the limestones are of shallow marine origin and are petrographically named as fusuline-bryozoan-echinoderm-molluscan wackestone, packstone and grain-

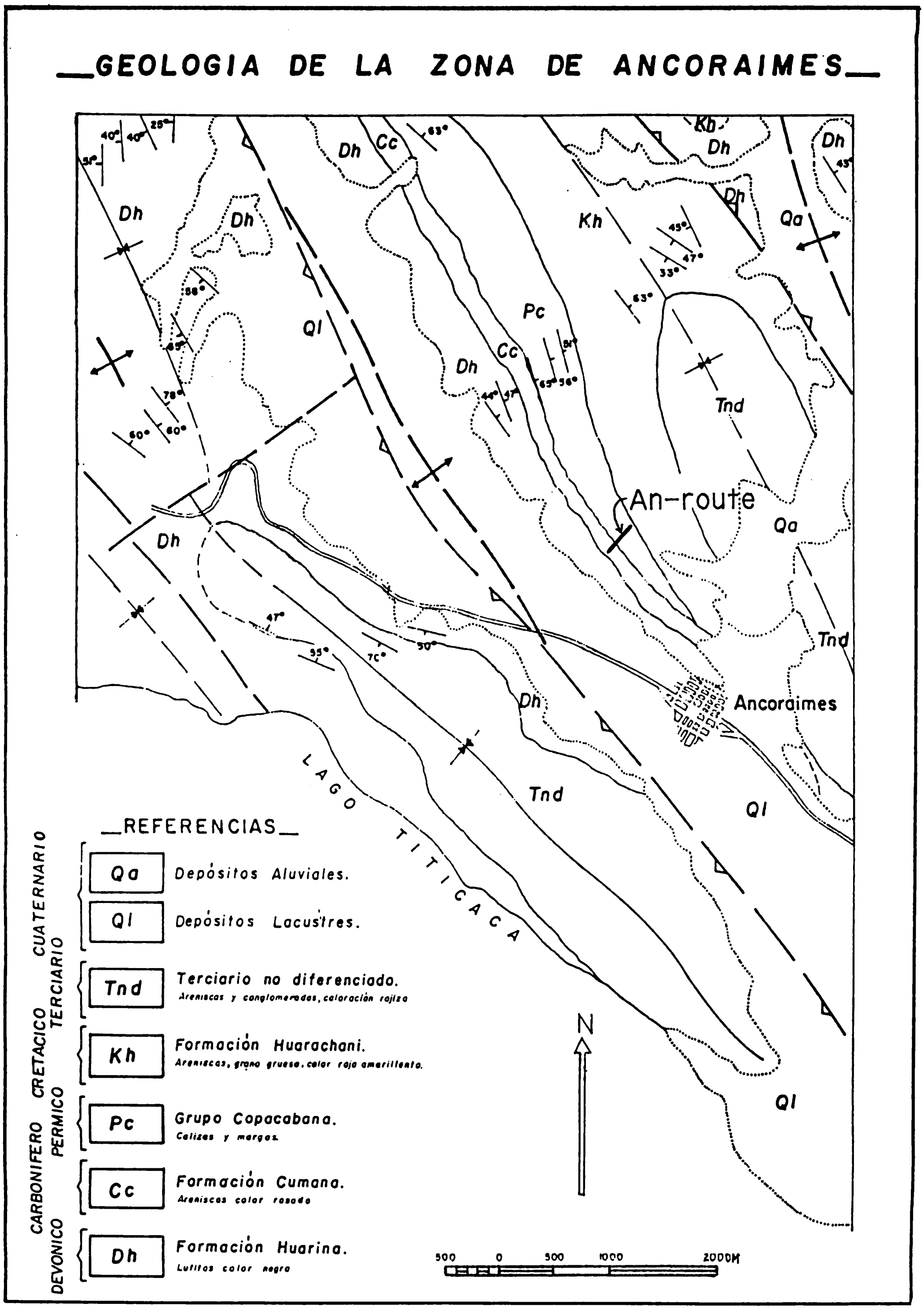


Figure 5. Geological map of the Ancoraimes area (by GEOBOL), showing the Ancoraimes (An) section.

stone. Dolomitization and silicification (chertification) of limestone are striking. The dolostone and nodular chert are regarded as final products of diagenetic processes, because the original texture of the limestone can be recognized easily in thin sections. The dolostone is made up of very fine- to fine- grained euhedral to subhedral interlocking dolomite crystals and the relics of original skeletal grains. The chert consists of chalcedonic and/ or microcrystalline quartz crystals. Both dolomite and chert are dominant in the upper part of the formation. The dolostone assumes a reddish-purple color, because dolomite crystals are rimmed with secondary iron minerals. The thickness of the Copácabana Group is about 215 m in Ya-route, and the general strike and dip are N40°-50°W and 60°-80°S, respectively. This group is overlain unconformably by a conglomerate which has been considered to be of Cretaceous age. However, because the mode of formation of this conglomerate differs distinctly from the Cretaceous developed in this region, we (Sakagami *ed*., 1984) have been inclined to think it to be of Tertiary age. The conglomerate comprises mainly rounded and subangular pebbles of sandstone, rarely limestone and chert. The pebbles varies from several millimeters to 20 cm in diameter. The matrix is generally a red-colored sandstone. Brachiopod shell fragments derived from the Copacabana Group are rarely found in the conglomerate.

A small hill, situated at about 2.5 km southeast of Cerro Jacha Khatawi (Figure 3), is considered by us to be the type locality of the brachiopods originally described by D'Orbigny. Wilson (1990), however, reported that this hill cannot be D'Orbigny's locality, based on D'Orbigny's (1842) description. In this small hill, only the Copacabana Group crops out, and the base and top are obscured ; the thickness is about 72 m. The general strike is N25°-30°W and the dip is 50°-60°S in the lower part but gradually decreasing (20°-30°S) upward. Generally, well stratified dolomitic limestone is predominant, with associated mudstone and shale beds. The dolomite is a reddish purple or yellowish brown color. Many fossils, such as fusulines, bryozoans, brachiopods, crinoids, corals and gastropods, commonly occur throughout the formation.

(2) Ancoraimes

At about 1 km north of Ancoraimes (village), Devonian and Carboniferous strata and the Copacabana Group are well exposed (Figure 5).

The Devonian consists of thick, hard, medium-grained, gray-colored sandstone with a strike and dip of N48°W and 58°N, respectively, and is easily recognizable by its topographically projected distribution.

The Carboniferous strata about 24 m thick overlie unconformably the Devonian beds with a strike and dip of N45°W and 40°-54°N, respectively, and consist mainly of gray or bluish-gray siltstone-shale with five horizons of fine-grained sandstone beds, 20 cm to 30 cm thick.

The Copacabana Group is considered to overlie the Carboniferous strata with angular unconformity and its upper limit is not exposed. We measured a 175 m-thick stratigraphic section. The strike and dip are about N60°W and 50°-60°N in the lower part and N70°W~E-W and 70°N~60°-80°S (reversed) in the upper part. This group can be divided lithologically into two parts : the lower part (An01-An28 ; 0 m-75 m) consists mainly of mudstone-shale beds associated with massive, gray to brown limestone-marl beds in which many brachiopods and rare fusulines are found ; the upper part consists mainly of massive, pale pink to reddish purple limestone-marl beds with some mudstone-shale and sandstone. In the upper part of the group, siliceous nodules that may have been produced by diagenesis are frequently observed and many fossils, such as fusulines, bryozoans, brachiopods and gastropods, are abundant.

(3) Matilde

Devonian, Carboniferous, Permian, Cretaceous and Tertiary strata are well distributed along the road to Matilde Mine from the lodging center situated at about 4 km southeast of the town of Carabuco (Figure 6).

The uppermost part of the Carboniferous Group near the base of the Copacabana Group consists of fine- to medium-grained, gray sandstone with well-developed cross-laminae. The strike and dip are N20°-30°W and 60°E, respectively. The direct relationship between the Carboniferous and Copacabana Group is not clear because of lack of outcrops.

The Copacabana Group is about 203 m thick, with a general strike and dip of N30°-35°W and 55°-60°N, respectively, and is unconformably overlain by Cretaceous strata. Lithologically, this group is subdivisible into two parts. The lower part (Ma01-Ma23 ; 0-75 m) consists of sandstone, siltstone, shale, marl and cherty rock, in which clastic rocks predominate. The limestone and marl are interbedded only with shale (gray to dark gray) and contain brachiopods, fusulines, corals, and other fossils. In the upper part (Ma24-Ma78 ; 75-203 m), dolomite and siliceous mudstone are predominant, with some sandstone, shale and limestone. The dolomite is reddish-purple and composed of fine- to medium-grained dolomitic crystals, and is characterized by fossil remains. The limestone alternates with shale or rather thick dolomite beds. The limestone between the dolomite beds is reddish purple. These limestones are composed of very coarse calcareous grains and brachiopods, bryozoans, fusulines, crinoids, and other fossils. The siliceous mudstone contains green glauconite and/or purple hematite and many trace fossils. There are slump structures in the limestone beds (Ma12-Ma13) and ripple marks in the limy sandstone layer (Ma60).

The Cretaceous overlies the Copacabana Group, and consists of massive, reddish mudstone. The strike and dip are N-S and 28°E, respectively.

(4) Cuyavi

Cuyavi is a small village situated about 20 km west of Yaurichambi and about 10 km northwest of the town of Ayagachi (Figure 7). A poor road alongside the lake

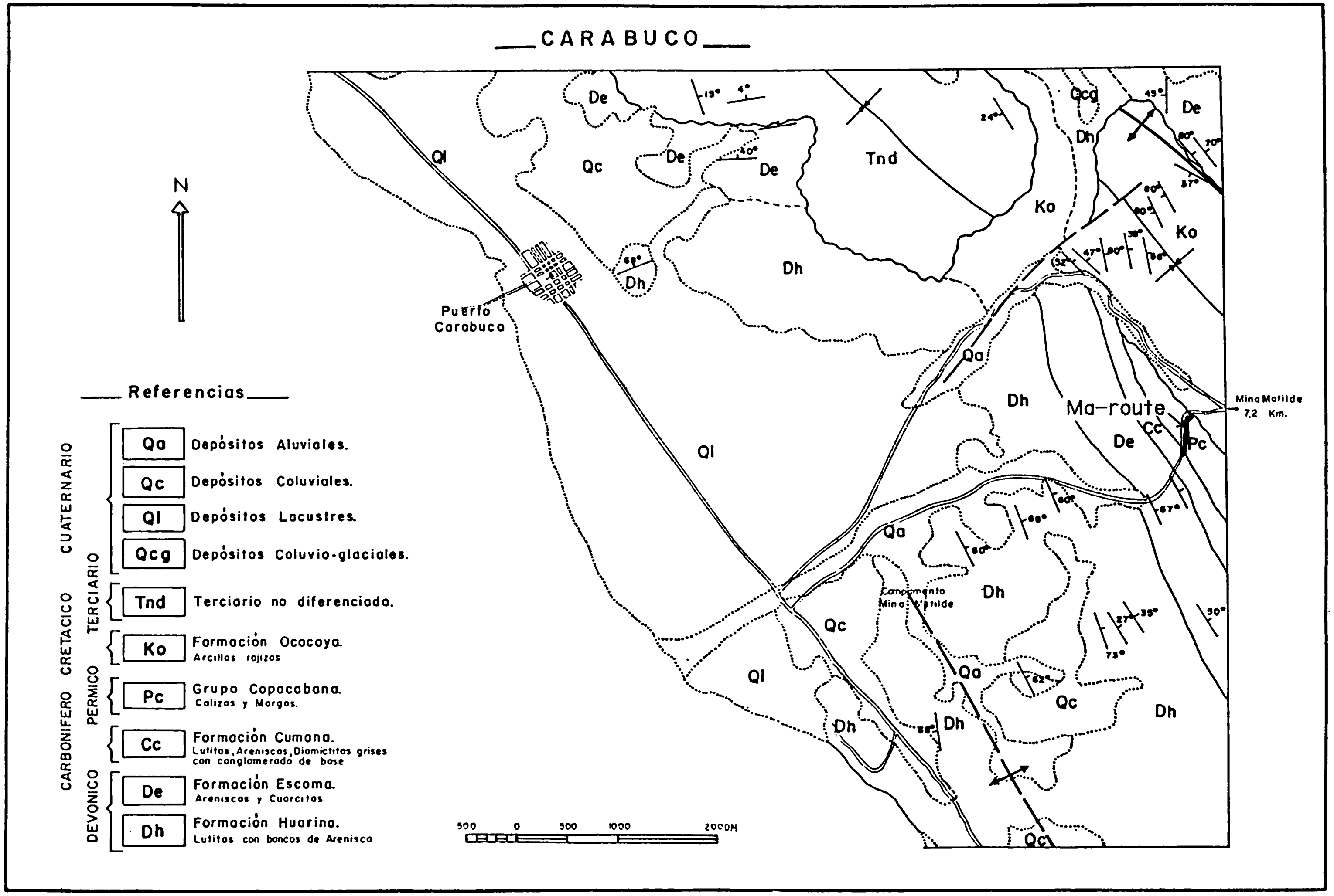


Figure 6. Geological map of the Carabuco area (by GEOBOL), showing the Matilde (Ma) section.

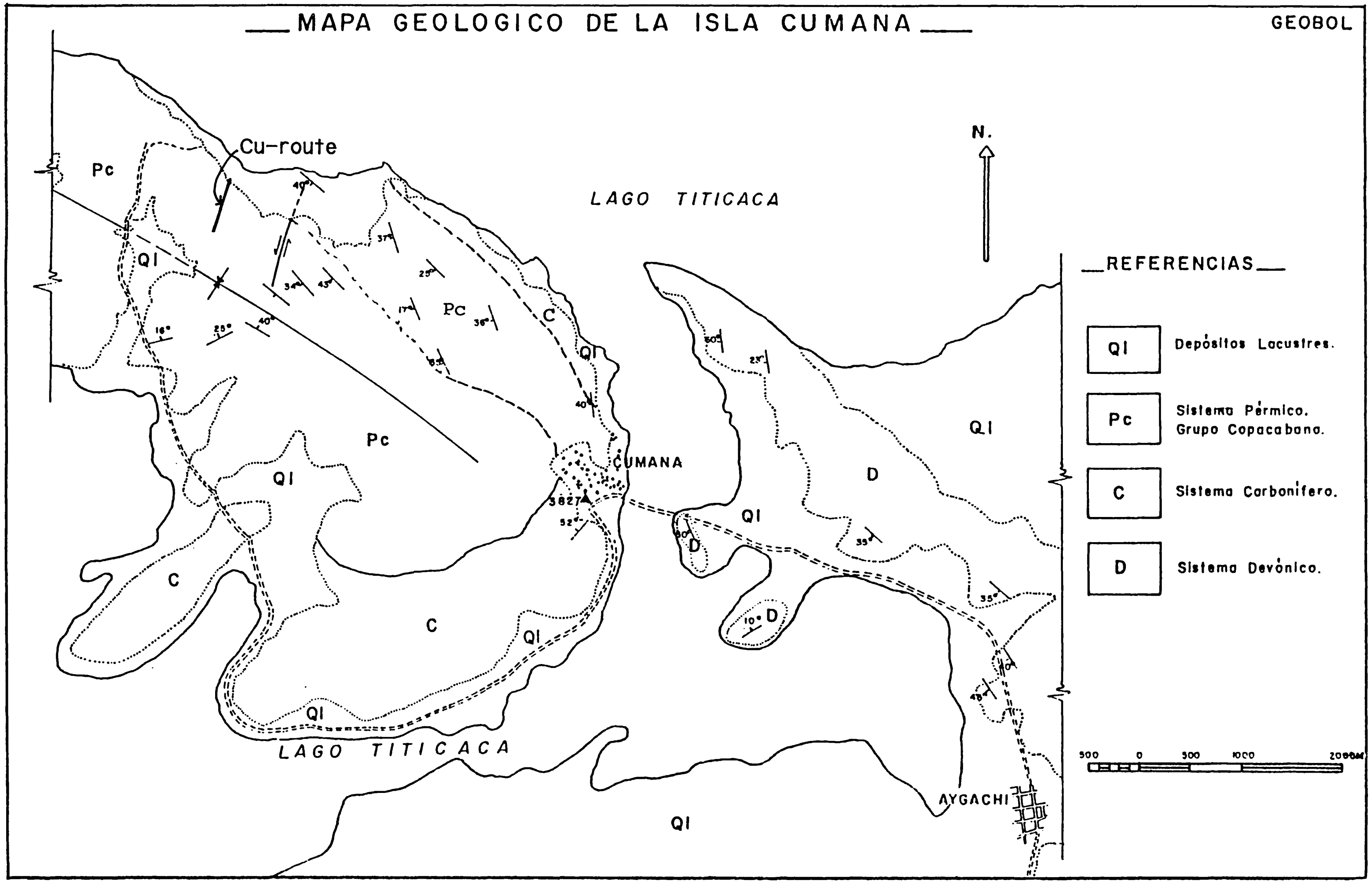


Figure 7. Geological map of Cumana Island (by GEOBOL), showing the Cuyavi (Cu) section.

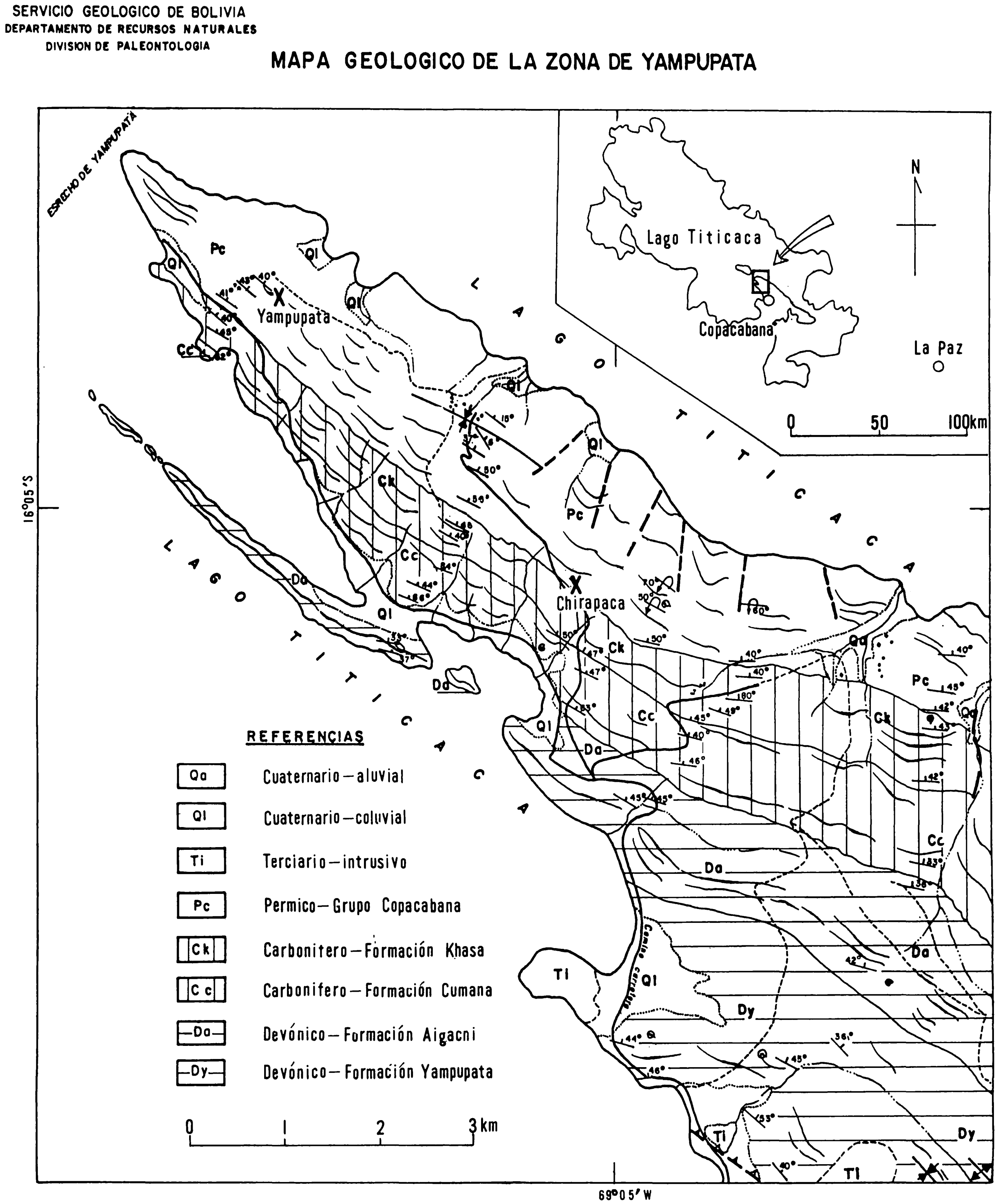


Figure 8. Geological map of the Yampupata area (by GEOBOL), showing the Yampupata (Yp) section and Chirapaca.

connects Aygachi to Cuyavi, via a bridge between Hacienda Yayes and Hacienda Cumana. The Copacabana Group is well developed on the northeastern slope of the mountain ridge. A synclinal axis runs parallel to the ridge so the formation dips to the southwest. The Carboniferous Gondwana Series is considered to overlie unconformably the lower units, but the direct relationship cannot be observed. The Gondwana Series consists mainly of massive, grayish-white coarse sandstone (quartzose arenite) and grayish-green medium-graind sandstone, with a thin alternation of shale and marl (10 cm-30 cm thick) in the uppermost part. Cross-bedding is well developed in the sandstone member. No fossils are observed. The relationship between the Carboniferous unit and the Copacabana Group is not clear, but there may be a slight angular unconformity.

The Copacabana Group consists mainly of limestone, marl, dolomite and mudstone-shale associated sandstone and chert. The thickness of the group is about 380 m or more but the upper limit is not exposed. This group can be divided lithologically into three members. The lower member (Cu01-Cu67 ; 0-180 m) is predominantly limestone and marl with some mudstone, shale and sandstone. The limestone and marl are generally gray to dark gray, and bear fusulines, brachiopods, bryozoans and gastropods in some horizons. The middle member (Cu68-Cu80 ; 180-260 m) consists of dolomite, mudstone and shale, including marl layers in several horizons. The dolomite is pinkish-brown to yellowish-brown, but occasionally it is white or grayish and consists of grains finer than silt. The mudstone and shale are gray, yellowish-brown, purple, pale green and greenish-blue. This member lacks fossils. The upper member (Cu81-Cu117 ; 260-380 m) is predominantly limestone and marl with some dolomite, sandstone, mudstone-shale and chert. The limestone and marl are gray to dark gray and contain brachiopods, bryozoans, corals, crinoids and fusulines. Corals are abundant in Cu81, bryozoans in Cu113 and fusulines in Cu117. As a whole, the pale green to greenish-blue mudstone-shale-sandstone beds which contain much quartz, feldspar, illite and glauconite grains are characteristic of the Copacabana Group in this area. Such mudstone-shale-sandstone beds are observed at two horizons in the lower part, six horizons in the middle part and four horizons in the upper part.

(5) Yampupata

As shown in the geological map (Figure 8), the Devonian, Carboniferous and Copacabana Groups are in succession along the southwestern slope of the mountain ridge. These strata occupy the southern limb of a syncline with a NW-SE trend.

The Carboniferous Gondwana Series about 50 m thick consists of medium- to coarse-grained, pale green sandstone with a general strike and dip of N45°-60°W and 50°N, respectively.

The Copacabana Group is more than 340 m thick, but the upper limit is not confirmed ; the general strike and dip are N45°-50°W and 35°-40°N, respectively. The relationship between the Carboniferous Gondwana Series and Copacabana Group may be a slight angular unconformity. This group consists of muddy limestone, marl, mudstone-shale and sandstone. The limestone and marl are mainly gray to dark gray, but some beds are partly brown and they contain many brachiopods, bryozoans, fusulines, etc. The mudstone-shale is a pale green color and is commonly siliceous. Generally, fossils are limited in occurrence. However, abundant bivalves associated with some brachiopods and rare bryozoans and ammonites occur in the green mudstone of the upper part of Yp26 bed. The sandstone is pale green, fine- to medium-grained, rarely coarse-grained, and without fossils. The Yp57 to Yp65 beds are fossiliferous, especially with fusulines in Yp57 and Yp62, and bryozoans and brachiopods in Yp65.

3. Faunal assemblages and age

The Copacabana Group in this region has four fusuline zones, namely from lower to upper, the *Profusulinella, Triticites, Pseudoschwagerina* and *Eoparafusulina* zones.

Eight stratigraphic sections are summarized in Figure 2. The two sections at Cuyavi and Yampupata are different in sedimentary characteristics, especially in the lower part of the group. In the Cuyavi and Yampupata sections, Sakagami and Mizuno (1994) discovered fusulines and conodonts indicating an Atokan age but these fossils are missing in other routes. The fusulines found at Cu46a and Cu46b horizons in the Cuyavi section and also in a float collected around Yp10 horizon in the Yampupata route include *Profusulinella munda* and *Profusulinella* sp. indet. Conodonts are known from several horizons from Cu04 to Cu46a in the Cuyavi section. The boundary between this *Profusulinella* zone (Atokan) and the *Triticites* zone (Virgilian) is still obscure, and the total thickness of these two zones is about 280 m in the Cuyavi section and 240 m in the Yampupata section.

The *Triticites* zone is recognized in three sections, Cerro Jacha Khatawi, Ancoraimes and Matilde, and its thickness is from 25 m to 40 m. This zone is poorly developed in the Cuyavi and Yampupata sections because fusulines and other fossils are very rare.

The *Pseudoschwagerina* zone is generally about 50 m thick but it is estimated to be more than 90 m in the Cuyavi section. The occurrence of the gastropod *Omphalotrochus* near the base of the *Pseudoschwagerina* zone is most characteristic and it is widely distributed at Yt10, Yc08, Yb11a, Ya10a, An12, Ma13, Cu96 and Yp61. Fusulines, brachiopods and bryozoans commonly occur in many horizons.

In the upper part of Cerro Jacha Khatawi (Ya, Yb. and Yc routes), and Ancoraimes and Matilde sections, the *Eoparafusulina* zone is thicker than the lower two fusuline zones but the exact thickness of the zone is uncertain. The thickness of the *Eoparafusulina* zone can be measured only in the Ya section at Cerro Jacha Khatawi, where it is about 130 m thick from the base to the boundary with the Tertiary. In the Cuyavi section, the *Eoparafusulina* zone cannot be recognized within the area of our surveyed section. In this zone, a characteristic autochthonous bivalve, *Aviculopinna*, occurs in almost all horizons, but has not yet been confirmed in this Yt-section or Yb-section at Cerro Jacha Khatawi, Cuyavi and Yampupata.

As mentioned above, the Copacabana Group distributed around the Lake Titicaca may range in geological age from Atokan (early Middle Pennsylvanian) to Leonardian (early Middle Permian).

4. Analysis of bryozoan fauna

Chronic (in Newell *et al.*, 1949, 1953) described 18 species of nine genera of bryozoans from the Upper Paleozoic of Peru, of which 14 species of eight genera were from the Copacabana Group and four species of two genera were from the Pennsylvanian Tarma Group. Except for *Meekopora* sp. cf. *M. prosseri* and *Streblotrypa* sp., twelve bryozoan species from the Copacabana Group

Table 1. Distribution of the bryozoans from the

Zones Species	Copacabana Group								
	Tr-Z			Ps-Z			Eo-Z		
	L	M	U	L	M	U	L	M	U
Genus *Fistulipora*									
F. incrustans				0	0				
F. cf. *F. timorensis*						0			
F. carrascoi sp. nov.					0				
F. titicacaensis sp. nov.					0				
F. multidiaphragma sp. nov.							0		
F. sp. indet. A			0						
F. sp. indet. B				0					
F. sp. indet. C						0			
F. sp. indet. D		0							
Genus *Meekopora*									
M. prosseri						0			
M. sp. indet.							0	0	
Genus *Goniocladia*									
G. peruviana		?	0	0					
Genus *Stenodiscus*									
S. altiplana sp. nov.							0		
Genus *Rhombotrypella*									
R. typica				0	0	0	0	0	?
R. aff. *R. gigantea*							0		
R. ? sp. indet.			0						
Genus *Tabulipora*									
T. cf. *T. carbonaria*				0					
T. sp. indet.						0			
Genus *Dyscritella*									
D. tenuirama							0	0	
D. aff. *D. komukensis*							0		
Genus *Pseudobatostomella*									
P. micropora sp. nov.							0	0	
P. yanagidai sp. nov.							0		
P. sp. indet.							0		

Tr-Z : *Triticites* zone, Ps-Z : *Pseudoschwagerina* zone, Eo-Z : *Eoparafusulina* zone, were differentiated as new. However, all the specimens identified and described by Chronic were etched silicified specimens. Chronic compared the bryozoan fauna with those of the North American Pennsylvanian to Lower Permian. Rowett (1975) recognized a remarkably high degree of similarity between Early Pennsylvanian and Early Permian invertebrates of northwestern South America and the southern Midcontinent of North America. He figured that in South America there are six endemic bryozoan species and six bryozoan species which are conspecific or have affinities with the North American Midcontinent fauna.

This study reports the distribution of 15 genera and 45 species from the Copacabana Group in the Lake Titicaca region, which is shown in Table 1. Bryozoans are absent in the lower part of the Copacabana Group in the *Profusulinella* and lower part of the *Triticites* zones. Only two species, *Fistulipora* sp. indet. D and *Alternifenestella*

Copacabana Group in the Lake Titicaca region.

Zones / Species	Copacabana Group								
	Tr-Z			Ps-Z			Eo-Z		
	L	M	U	L	M	U	L	M	U
Genus *Rhombopora*									
R. lepidodendroides			0		0	0		0	
R. corticata				0		0			
R. kawabei sp. nov.							0		
Genus *Streblotrypa*									
S. sp. indet.						0			
Genus *Alternifenestella*									
A. minor			0	0					
A. aff. *A. pajerensis*		0		0					
A. (*C.*) *cervoides*					0				
A (*C.*) *aspera*				0					
A. ? sp. indet.			0						
Genus *Minilya*									
M. binodata				0					
Genus *Fabifenestella*									
F. aff. *F. huascatayana*			0						
F. sp. indet.			0	0					
Genus *Polypora*									
P. elliptica						0	0		
P. cyclopora					?	0	0		
P. aff. *P. inimica*							0	?	
P. cf. *P. megastoma*			0	0	0	?			
P. sp. indet. A							0		
P. sp. indet. B					0				
P. sp. indet. C							0		
Genus *Septopora*									
S. andeana sp. nov.						0			
S. lineata							0		
S. incaica							0		

L : Lower, M : Middle, U : Upper.

aff. *A. pajerensis*, are recognized in the middle part of the *Triticites* zone.

Higher, the number of bryozoan species rapidly increases. Nine species occur in the upper part of the *Triticites* zone, 12 species in the lower part of the *Pseudoschwagerina* zone, 10 in the middle part, and 12 in the upper part. After reaching a climax (18 species) in the lower part of the *Eoparafusulina* zone, the number of species rapidly decreases to six species in the middle part, and only one species, *Rhombotrypella typica* ?, occurs in the upper part of the *Eoparafusulina* zone.

Among the nine species of the genus *Fistulipora, F. incrustans* was originally described from the Pennsylvanian Graham Formation of north central Texas and later also from the Wreford Megacyclothem (Wolfcampian) of Kansas. It is noteworthy that both *Fistulipora* cf. *F. timorensis* and *F. carrascoi* sp. nov. are closely related to the Tethyan species *F. timorensis*, described originally from Timor Island, and *F. hamadae*, described from peninsular Thailand, respectively. The other two new species, *F. titicacaensis* and *F. ? multidiaphragma* are readily distinguished from the two previously described species.

The Bolivian specimens of *Meekopora prosseri* are identical with the material which was originally described from the Coal Measures of Nebraska and later from the Upper Pennsylvanian to Lower Permian in the Midcontinental region of North America. *M. prosseri* may be cosmopolitan because it is known not only from the Copacabana Group in Peru (Chronic in Newell *et al*., 1949, 1953), but also from the Permian of the Tethyan province, for example the Mt. Everest (Chomolungma) region, southwestern China (Yang and Xia, 1981) and Afghanistan (Termier and Termier, 1971).

One species of the genus *Goniocladia, G. peruviana,* described in the study, is identical to the original specimens which were described from the Copacabana Group in Peru, and it may be related to *G. americana* from the Guadalupian of Texas, U.S.A. (Girty, 1908) and *G. timorensis* from the Permian of Timor Island (Bassler, 1929).

Stenodiscus altiplana is a new species, but the genus *Stenodiscus* had not previously been reported from the Lower Permian of the Midcontinent province (Ross and Ross, 1990). *Tabulipora carbonaria* is widely distributed from the Middle Pennsylvanian to Lower Permian in the Midcontinent (Cuffey, 1967). The genus *Rhombotrypella* extends from the Russian platform via the North American Cordillera into Bolivia in the Upper Carboniferous and Lower Permian. The genera *Dyscritella* and *Pseudobatostomella* are recorded for the first time from the Copacabana Group but they are very common in the Tethyan province.

The genus *Rhombopora* is very common in the Carboniferous to Permian of the Midcontinent province, especially *Rhombopora lepidodendroides* which is widely distributed along with *Fistulipora incrustans* and *Tabulipora carbonaria* in the Wreford Megacyclothem (Wolfcampian) of Kansas. The genus *Streblotrypa* seems to be very limited in its occurrence in the Copacabana Group of this region.

Eighteen species of fenestellid bryozoans are identified including five species of *Alternifenestella*. Three of these species are indeterminable and the fourth species was described by Chronic (in Newell *et al*., 1949,1953) from the Copacabana Group in Peru. The other species, *A. minor*, was originally described from the Russian Platform province.

The species *Minilya binodata* described in this study may be identical with the type *binodata* which was described by Condra (1902) from the upper Virgilian Shawnee Group of Nebraska. Of two species of the genus *Fabifenestella*, one has affinities with *F. huascatayana* described originally by Chronic (in Newell *et al*., 1949, 1953) from the Copacabana Group in Peru and the other is an indeterminable species.

Among seven species of the genus *Polypora*, three are indeterminable. *Polypora* aff. *P. inimica* may be identical with the originally described species from the Copacabana Group in Peru, and *Polypora elliptica* in the study agrees with *P. elliptica* (s.s.) described by Elias (1937) in meshwork measurements and essential characters. *Polypora cyclopora* was originally described from the European part of Russia and *Polypora* cf. *P. megastoma* is very similar to the specimens from the Middle *Productus* limestone of Pakistan.

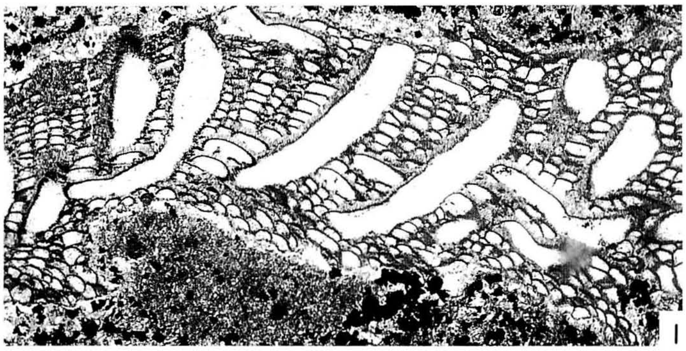
Of three species of *Septopora, S. incaica* is already known from the Copacabana Group in Peru. *S. andeana* is a new species and *Septopora lineata* was originally described from the Lower Guadalupian of Armenia.

Of the named 31 species, eight species are new, eight are endemic Andean species, seven are common to those of the Midcontinent region and eight are in the Tethyan province. The Tethyan association is considered to be significant. Lohmann (1970) suggested that "The Copacabana transgression may be regarded as part of the major (eustatic?) post-Gondwana transgression which spread from the warm equatorial Tethys sea over the Gondwanaland margins, as evidenced by the presence of corals and *Productus*-bearing limestones. Similar transgressions are known elsewhere, for example, in the Salt Range of Pakistan and India where the famous *Productus* beds overlie the Gondwana glacial section".

Systematic paleontology

All specimens are deposited in the collections of the Department of Earth Sciences, Faculty of Science, Chiba University (DESC-). Symbols and numbers in parenth-

Figure 9. **1, 2.** *Fistulipora incrustans* Moore, longitudinal and tangential sections, ×20, DESC-95032 (Ya12a-21) and DESC-95029 (Ya12a-17), respectively. **3, 4.** *Fistulipora* cf. *F. timorensis* Bassler, longitudinal and oblique sections, ×20, DESC-95142 (Ma32-1a) and DESC-95145 (Ma32-4a), respectively. **5, 8.** *Fistulipora* sp. indet. B, oblique sections, ×20, DESC-95019 (Ya12a-6b) and DESC-95022 (Ya12a-9a), respectively. **6.** *Fistulipora* sp. indet. A, longitudinal section, ×20, DESC-95006 (Ya07-2a). **7.** *Fistulipora* sp. indet. C, tangential section, ×20, DESC-95093 (Yc16-1a).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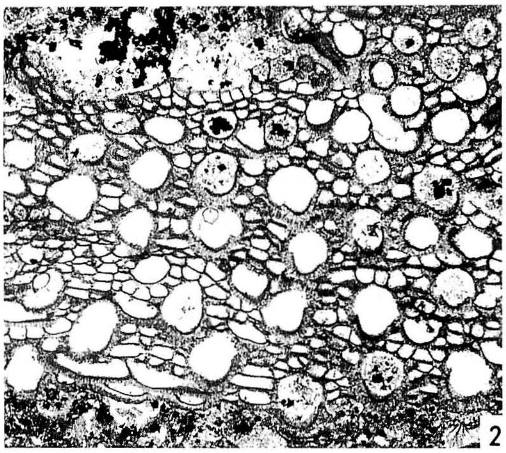
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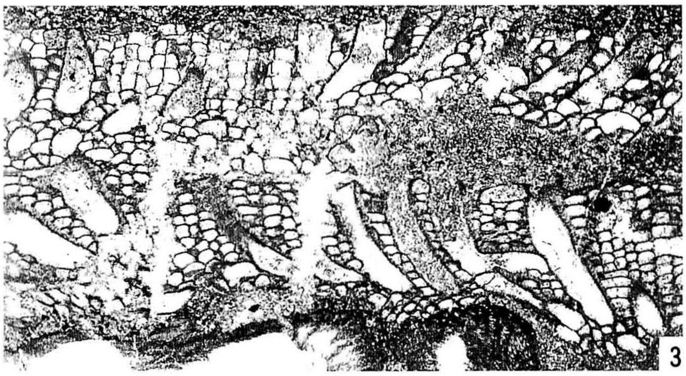
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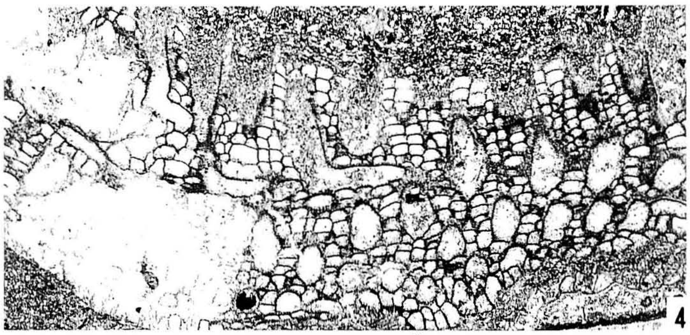
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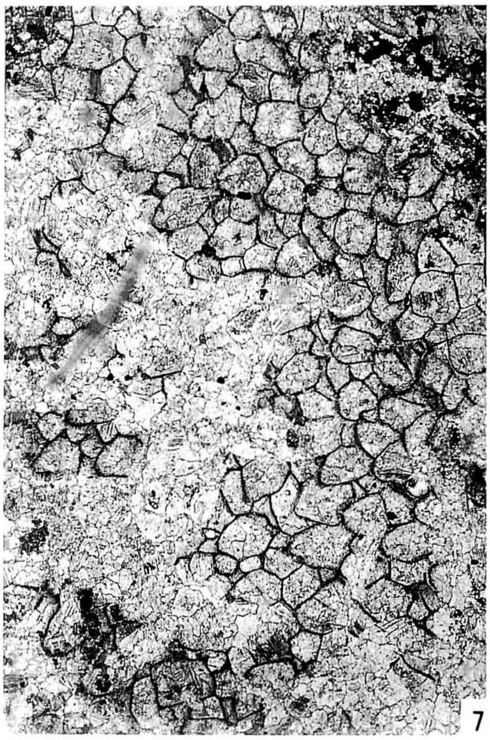
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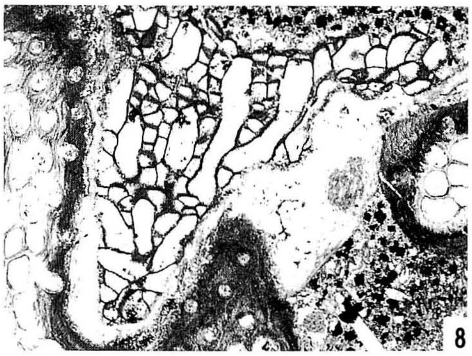
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eses show the locations and horizons.

Order Cystoporata Astrova, 1964
Suborder Fistuliporina Astrova, 1964
Family Fistuliporidae Ulrich, 1882
Genus ***Fistulipora*** McCoy, 1949

Fistulipora incrustans Moore, 1929

Figures 9-1, 2

Fistulipora incrustans Moore, 1929, p. 3, 4, pl. 1, figs. 1, 2, 6, 8; Warner and Cuffey, 1973, p. 8-11, figs. 1-7.

Material.—DESC-95029 (Ya12a-17), DESC-95032 (Ya12a-21), DESC-95227 (Yp65-24).

Horizon.—Lower to middle part of *Pseudoschwagerina* zone in Yaurichambi-a and Yampupata routes.

Description.—Zoarium may have been attached to a foreign object such as seaweed.

In tangential section, zooecial tube broadly ovate or subcircular, longer diameter excluding lunarium ranges from 0.256 to 0.384 mm and shorter diameter from 0.205 to 0.346 mm. Usually 4 zooecia per 2 mm diagonally. Lunarium occupies about one third of zooecial circumference, its thickness from 0.064 to 0.102 mm. Vesicular tissue consists of fine vesicles regular in size, one to three vesicles between adjacent zooecia. Usually 7 to 8 vesicles per mm horizontally.

In longitudinal section, zooecial tube parallel to coenelasma for a short distance and curved gradually upward, forming with outer surface of zoarium an angle of about 90°. Diaphragms absent. Interzooecial tissue consists of regularly arranged vesicles which are usually quadrate but some are depressed, elongated, or irregularly shaped. 11 to 14 vesicles per mm longitudinally.

Remarks.—Except for being slightly thicker, the colonies are identical with *Fistulipora incrustans*, which was originally described from the Graham Formation (Pennsylvanian) of north-central Texas by Moore (1929) and later from the Wreford Megacyclothem (Lower Permian) by Warner and Cuffey (1973), in essential characters.

Fistulipora cf. ***F. timorensis*** Bassler, 1929

Figures 9-3, 4

Fistulipora timorensis Bassler, 1929, p. 44, pl. CCXXVII(3), figs. 4-9.

Material.—DESC-95142 (Ma32-1a), DESC-95143 (Ma32-2a), DESC-95144 (Ma32-3a), DESC-95145 (Ma32-4a), DESC-95146 (Ma32-5a).

Horizon.—Lower part of *Eoparafusulina* zone in Matilde route. Associated fossils include *Rhombotrypella, Tabulipora, Dyscritella, Polypora* and *Aviculopinna*.

Description.—Zoarium encrusts both sides of *Polypora* sp. indet. C and is a thin layer, varying from 1.3 to 2.3 mm in thickness; occasionally multiple layers present.

In tangential section, zooecial tube broadly ovate or subcircular, longer diameter excluding lunarium from 0.218 to 0.230 mm and shorter diameter from 0.154 to 0.192 mm. Usually 5.5 to 6 zooecia per 2 mm diagonally. Lunarium well developed, horseshoe-shaped, occupying one-third to nearly one-half of zooecial circumference, its thickness usually about 0.038 mm, but occasionally up to 0.064 mm. Vesicular tissue fine and regular in size, one to three vesicles between adjacent zooecia. Usually 7 to 8 vesicles per 1 mm horizontally.

In longitudinal section, zooecial tubes parallel to coenelasma for a short distance and then curved upward, making a right angle to zoarial surface. Diaphragm absent. Interzooecial tissue consists of regularly arranged vesicular tissue which is depressed quadrate. 10 to 13 vesicles per 1 mm longitudinally.

Remarks.—The colonies are similar to *Fistulipora timorensis* Bassler in many respects, but slight differences in zooecial and zoarial measurements have led me to only compare these specimens with Bassler's species. *Fistulipora timorensis* was described originally by Bassler (1929) from the Permian of Timor Island, and subsequently has been described from many places, such as Japan and Thailand by Sakagami (1961, 1968), Khabarovsk region and Primorskiy Kray of Russia by Morozova (1970) and Xizang, China by Yang, Lu and Xia (1981). The colonies also resemble those of *Fistulipora incrustans*, but are distinguishable from the latter by the smaller size of the zooecial tube.

Fistulipora carrascoi sp. nov.

Figures 10-1—4; 11-1, 2

Material.—Holotype: DESC-95167 (Cu113-7); Paratypes: DESC-95163 (Cu113-1), DESC-95164 (Cu113-2), DESC-95165 (Cu113-3), DESC-95166 (Cu113-6), DESC-95214 (Yp65-10), DESC-95216 (Yp65-12), DESC-95218 (Yp65-15), DESC-95220 (Yp65-17), DESC-95222(Yp65-19), DESC-95223 (Yp65-20), DESC-95225 (Yp65-22), DESC-95226 (Yp65-23).

Horizon.—Middle part of *Pseudoschwagerina* zone in Cuyavi and Yampupata routes.

Description.—Zoarium ramose, diameter ranging from 6. 5 to 11 mm, and occasionally 13 mm.

In tangential section of mature zone, zooecial tubes nearly circular, with two constricted parts which correspond to the edges of the lunarium. Longest diameter of zooecium excluding lunarium ranges from 0.294 to 0.384 mm, shorter diameter from 0.256 to 0.333 mm. Usually 4 zooecia per 2 mm in diagonal direction.

In longitudinal section, zooecial tubes parallel to longitudinal direction in central region, but curved gradually outward, making a right angle in mature zone. Thickness of mature zone ranging from 1.0 to 1.5 mm. One or two diaphragms observable near the boundary between mature and immature zones. Interzooecial tissue in immature zone consists of very coarse vesicles, elongated quadrate or polygonal and irregular in size, but generally becoming fine and regular to outer region. Usually 6 to 7, occasionally 8 vesicles per mm longitudinally, and 5 to 6

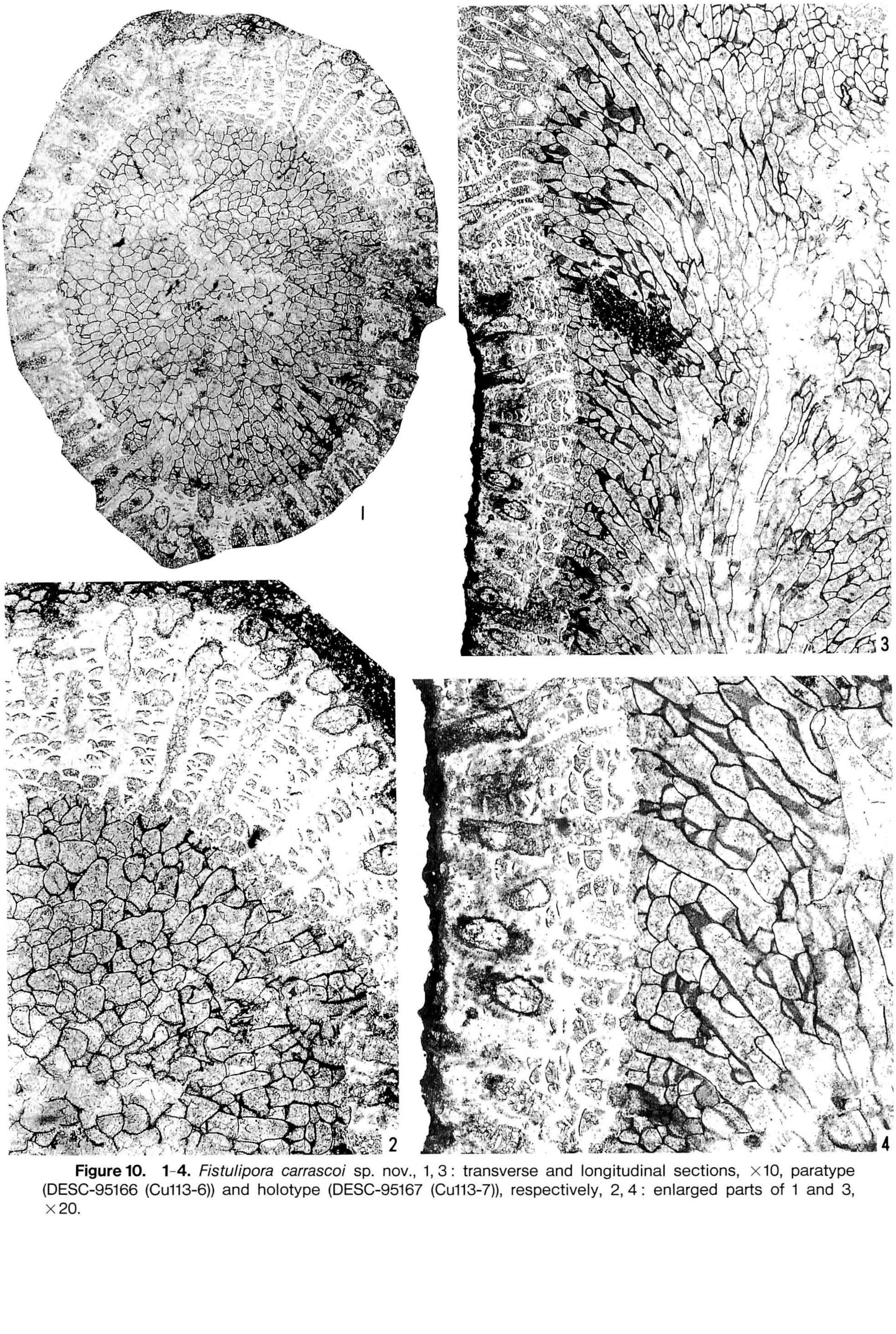


Figure 10. **1–4.** *Fistulipora carrascoi* sp. nov., 1, 3 : transverse and longitudinal sections, ×10, paratype (DESC-95166 (Cu113-6)) and holotype (DESC-95167 (Cu113-7)), respectively, 2, 4 : enlarged parts of 1 and 3, ×20.

per mm horizontally.

In transverse section, the tangential part of the immature zone and the longitudinal section of the mature zone can be observed.

Remarks.—The colonies are similar to those of *Fistulipora hamadae* which was described by Sakagami (1966) from the Middle Permian limestone of Ko Muk, peninsular Thailand, especially in the internal structure of the immature zones, however, they differ in the larger diameter of the zooecial tubes.

The specific name is dedicated to Dr. Raul Carrasco C., the former Director of the Servicio Geologico de Bolivia (GEOBOL), who kindly helped us during our field surveys in the Lake Titicaca region.

Fistulipora titicacaensis sp. nov.

Figures 11-3, 4

Material.—Holotype : DESC-95182 (Cu114-4) ; Paratypes : DESC-95184 (Cu114-6), DESC-95189 (Cu114-24), DESC-95193 (Cu114-31).

Horizon.—Middle part of *Pseudoschwagerina* zone in Cuyavi route.

Description.—Zoarium may have been attached to a foreign object such as seaweed.

In tangential section, zooecial tubes irregularly polygonal, with rounded corners. Shorter diameter usually ranges from 0.256 to 0.307 mm, occasionally to 0.384 mm at its maximum. Usually 3.5 to 4 zooecia per 2 mm diagonally. Lunarium present but occupying less than one-fourth of zooecial circumference. Very thin lunarium, less than 0.020 mm.

In longitudinal section, zooecial tubes parallel to coenelasma for a short distance and curved gradually upward, meeting outer surface of zoarium at an angle of about 90°. Diaphragms absent. Zooecial wall zigzag except for the side with lunarium which is straight. Vesicular tissue consists of regularly arranged vesicles which are usually depressed quadrate, 7 to 8 vesicles per mm longitudinally.

Remarks.—The present form is characterized by the irregularly zigzag wall of zooecial tubes and the small lunarium. It can be readily distinguished from the previously described species.

Fistulipora* ? *multidiaphragma sp. nov.

Figures 11-5—7

Material.—Holotype : DESC-95047 (Ya34-4) ; Paratypes : DESC-95052 (Ya35a-5), DESC-95053 (Ya35a-6).

Horizon.—Middle part of *Eoparafusulina* zone in Yaurichambi-a route.

Description.—Shape of zoarium uncertain but probably ramose, about 10 mm in diameter.

In tangential section, zooecial tubes nearly circular or oval, shorter diameter ranges from 0.256 to 0.384 mm, usually 4 to 5 zooecia per 2 mm diagonally. Vesicular tissue consists of coarse vesicles, usually one to two vesicles between adjacent zooecia. Lunarium indistinct.

In longitudinal section, zooecial tubes *gradually curved* outward and outer surface of zoarium nearly at right angles. Diaphragms abundant and regularly spaced throughout tube. Interspaces between diaphragms usually 0.192 mm to 0.320 mm. Vesicular tissue bubble-like, irregularly and coarsely developed only in mature zone and absent in immature zone.

Remarks.—The present form is characterized by lack of vesicular tissue in the immature zone and abundant, regularly spaced diaphragms throughout the tube. There is some doubt as to its generic assignment, however, the present form can be distinguished from any other described species.

Fistulipora sp. indet A

Figure 9-6

Material.—DESC-95006 (Ya07-2a), DESC-95007 (Ya08b-1).

Horizon.—Upper part of *Triticites* zone in Yaurichambi-a route.

Description.—Obliquely longitudinal and fragmentary tangential sections attached to sinoporid corals. Zoarium incrusting, composed of two layers in one specimen. Thickness of each zoarial layer less than 1 mm.

In tangential section, zooecial tube broadly ovate, shorter diameter from 0.256 to 0.333 mm. Usually 3 to 4 zooecia in 2 mm diagonally. Lunarium occupies about one-third of zooecial circumference, 0.051 to 0.064 mm in thickness.

In longitudinal section, zooecial tubes parallel to coenelasma for a very short distance and curved gradually upward, meeting outer surface of zoarium at an angle of about 90°. One slightly convex diaphragm observed near aperture of tube. Interspaces of zooecia consist of irregularly arranged vesicles.

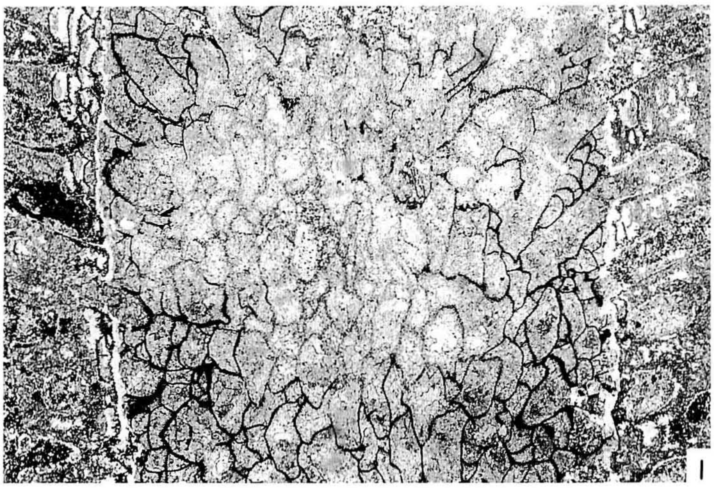
Remarks.—Specific identification is not made because of the poorly preserved sections and insufficient material. The present form somewhat resembles *Fistulipora incrustans.*

Fistulipora sp. indet B

Figures 9-5, 8

Material.—DESC-95019 (Ya12a-6a), DESC-95022

Figure 11. 1, 2. *Fistulipora carrascoi* sp. nov., tangential and longitudinal but slightly excentric sections, ×20, paratypes (DESC-95225 (Yp65-22a) and DESC-95223 (Ya65-20)). **3, 4.** *Fistulipora titicacaensis* sp. nov., longitudinal and tangential sections, ×20, holotype (DESC-95182 (Cu114-4)) and paratype (DESC-95189 (Cu114-24)), respectively. **5-7.** *Fistulipora ? multidiaphragma* sp. nov., tangential, longitudinal and oblique sections, ×20, holotype (DESC-95047 (Ya-34-4)), paratypes (DESC-95053 (Ya35a-6a and b)), respectively.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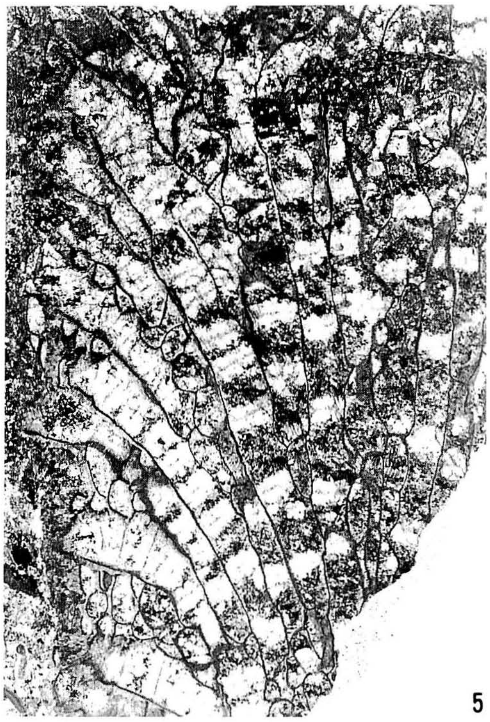
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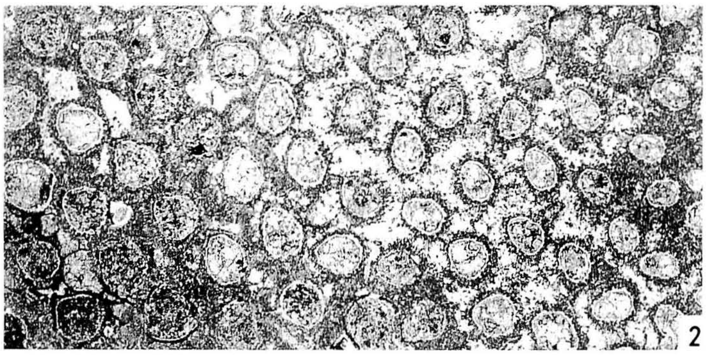
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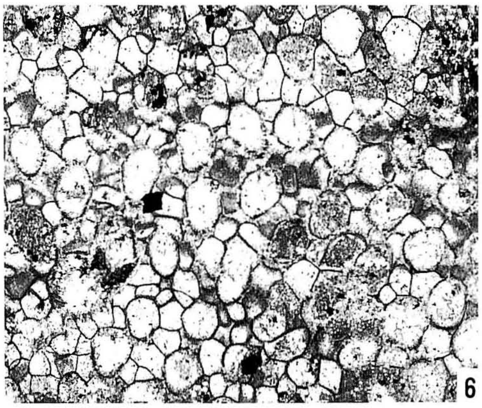
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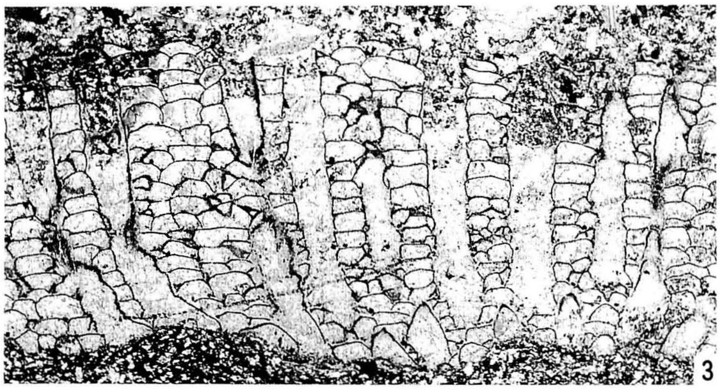
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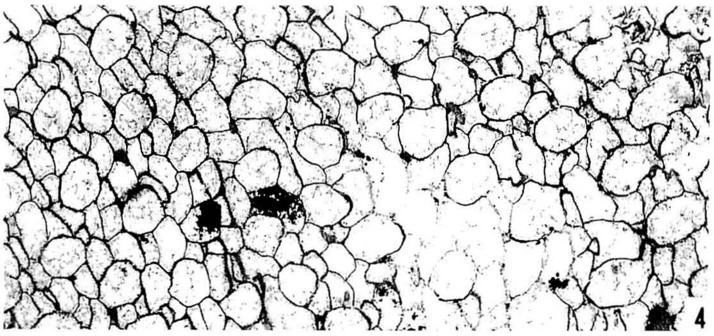
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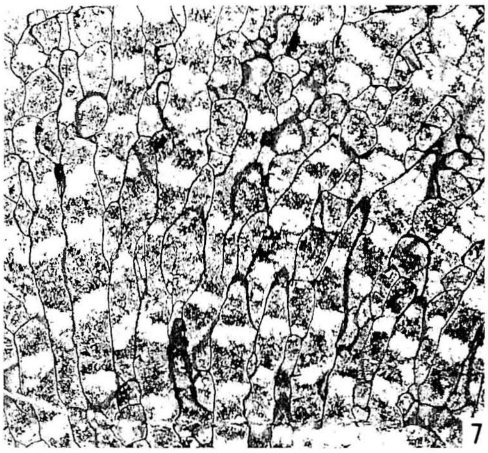
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(Ya12a-9a).

Horizon.—Lower part of *Pseudoschwagerina* zone in Yaurichambi-a route.

Description.—Two oblique sections attached to a brachiopod shell and zoarium of *Polypora*. Zoarium encrusting, consists of one layer; thickness not determinable. Zooecial tube probably circular, 0.192 mm in average diameter. Lunarium not strongly developed, occupies about one-fourth of zooecial circumference, less than 0.050 mm in thickest part. No diaphragm.

Remarks.—There is no specific identification because the specimens are fragmentary and poorly preserved.

Fistulipora sp. indet. C

Figure 9-7

Material.—DESC-95093 (Yc16-1a), DESC-95094 (Yc16-3a), DESC-95095 (Yc16-4).

Horizon.—Upper part of *Pseudoschwagerina* zone in Yaurichambi-c route.

Description.—Three tangential sections from one fragmentary zoarium. Zoarium probably encrusting, but the thickness not determinable. Zooecial tube broadly oval, longer diameter excluding lunarium less than 0.384 mm and shorter diameter from 0.256 to 0.307 mm. Usually 4 zooecia in 2 mm diagonally. Lunarium small and thin, about one-fourth of zooecial circumference. Usually one row of vesicular tissue, occasionally two rows of vesicles between adjacent zooecia.

Remarks.—Because of the poor presevation of the thin sections of the fragmentary zoarium, a specific identification is not possible.

Fistulipora sp. indet. D

Figures 12-1—4

Material.—DESC-95123 (Ma6-4a), DESC-95124 (Ma6 (0.5 m up)-2), DESC-95127 (Ma6 (0.5 m up)-6), DESC-95130 (Ma6 (0.5 m up)-9).

Horizon.—Middle part of *Triticites* zone in Matilde route.

Description.—Zoarium encrusting, consisting of about a 3 mm thick layer, may have been attached to a foreign object such as seaweed.

In tangential section, zooecial tubes nearly circular or oval, shorter diameter from 0.256 to 0.384 mm; usually 3 to 3.5 zooecia per 2 mm diagonally. Lunarium present but not prominent. Vesicular tissue consists of fine vesicles, regularly arranged, usually 2 to 3 vesicles between adjacent zooecia and 5 to 7 vesicles per mm horizontally.

In longitudinal section, zooecial tubes parallel to coenelasma for a short distance, curved gradually upward and then extending directly to outer surface of zoarium at an angle of about 90°. Diaphragm absent throughout tube. Vesicular tissue regularly arranged, usually quadrate, 6 to 7 vesicles per mm longitudinally.

Remarks.—This zoarium is closely similar to *Fistulipora incrustans* in its main characters, but it can be distinguished from *F. incrustans* by the less developed lunarium and coarser accumulation of vesicles.

Family Hexagonellidae Crockford, 1947
Genus **Meekopora** Ulrich, 1889

Meekopora prosseri Ulrich, 1902

Figures 13-2—5

Meekopora prosseri Ulrich in Condra 1902, p. 339, pl. 18, fig. 9, pl. 19, figs. 1-6; Condra, 1903, p. 36, pl. 3, figs. 1-7; Moore and Dudley, 1944, p. 299, 300, pl. 37, figs. 3, 4, pl. 38, figs. 1, 8, pl. 39, fig. 3, pl. 41, fig. 7, pl. 42, figs. 1-3, pl. 44, figs. 1, 2, pl. 45, figs. 1, 2, 4, pl. 46, figs. 4, 8; Warner and Cuffey, 1973, p. 14-19, pl. 3, figs. 1-6; Yang and Xia, 1975, p. 45, 46, pl. 3, figs. 5-7.

Meekopora cf. *prosseri* Ulrich. Termier and Termier, 1971, p. 27, pl. 11, figs. 1-3.

Meekopora cf. *M. prosseri* Ulrich. Chronic in Newell *et al*., 1953, p. 111, pl. 21, figs. 1, 2.

Material.—DESC-95168 (Cu113-9), DESC-95169 (Cu113-10), DESC-95170 (Cu113-11), DESC-95173 (Cu113-14), DESC-95175 (Cu113-16a, b), DESC-95176 (Cu113-17), DESC-95188 (Cu114-21), DESC-95194 (Cu114-33), DESC-95203 (Cu115-11), DESC-95204 (Cu115-13), DESC-95205 (Cu115-16), DESC-95207 (Cu115-18).

Horizon.—Upper part of *Pseudoschwagerina* zone in Cuyavi route.

Description.—Zoarial features are only seen in thin sections: probably broad, parallel-sided, flattened, bifurcating frond, 1.5 to 2.0 mm in thickness.

In tangential section, zooecial tubes nearly circular to oval, diameter from 0.141 or 0.205 mm, occasionally 0.320 mm at its maximum, usually 5 zooecia per 2 mm diagonally. Lunarium not observed. Interzooecial tissue is fine and regularly arranged, 7 to 8 vesicles per mm horizontally in inner zone, but occasionally covered by dark dense fibrous tissue.

In longitudinal section, zooecial tubes proximally parallel to mesotheca for some distance, then gradually curved upward, making a right angle with outer surface of zoarium. One to 2 diaphragms in inner part of zooecial tube. Vesicular tissue fine and regularly arranged, about 10 vesicles per mm longitudinally in outer zone.

Remarks.—Chronic (in Newell *et al*., 1953) described *Meekopora* cf. *M. prosseri* from two localities in the Andean region of Peru, but this was only from surface silicified specimens, and internal structure is unknown. This species, widely distributed in time and space, was described originally from the Coal Measures of Nebraska by Ulrich (in Condra, 1902), later from the Upper Pennsylvanian (Morrowan to Virgilian) to Lower Permian (Wolfcampian) of the Midcontinent region by Moore and Dudley (1944) and from the Wreford Megacyclothem (Lower Permian) of Kansas by Warner and Cuffey (1973). The present species was reported also from the Permian of the Everest region (southwestern China) by Yang and Xia (1975) and of Afghanistan by Termier and Termier (1971).

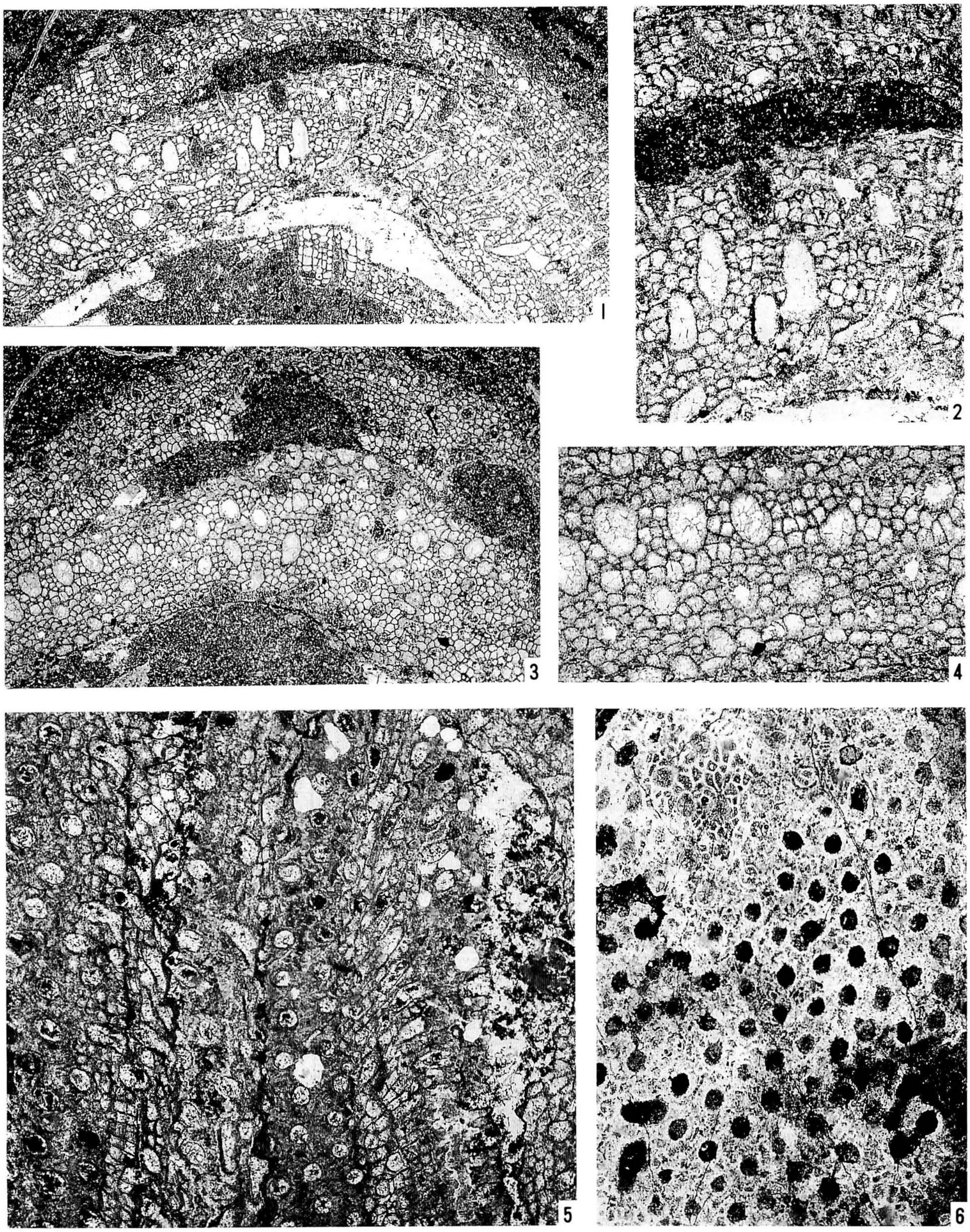

Figure 12. 1–4. *Fistulipora* sp. indet. D, 1, 3 : obliquely longitudinal and tangential sections, ×10, DESC-95130 (Ma6 (1.5 m up)-9) and DESC-95124 (Ma6 (1.5 m up)-2), respectively, 2, 4 : enlarged parts of 1 and 3, ×20. **5, 6.** *Meekopora* sp. indet., obliquely longitudinal and tangential sections, ×20, DESC-95068 (Ya39a-3) and DESC-95119 (An40-5), respectively.

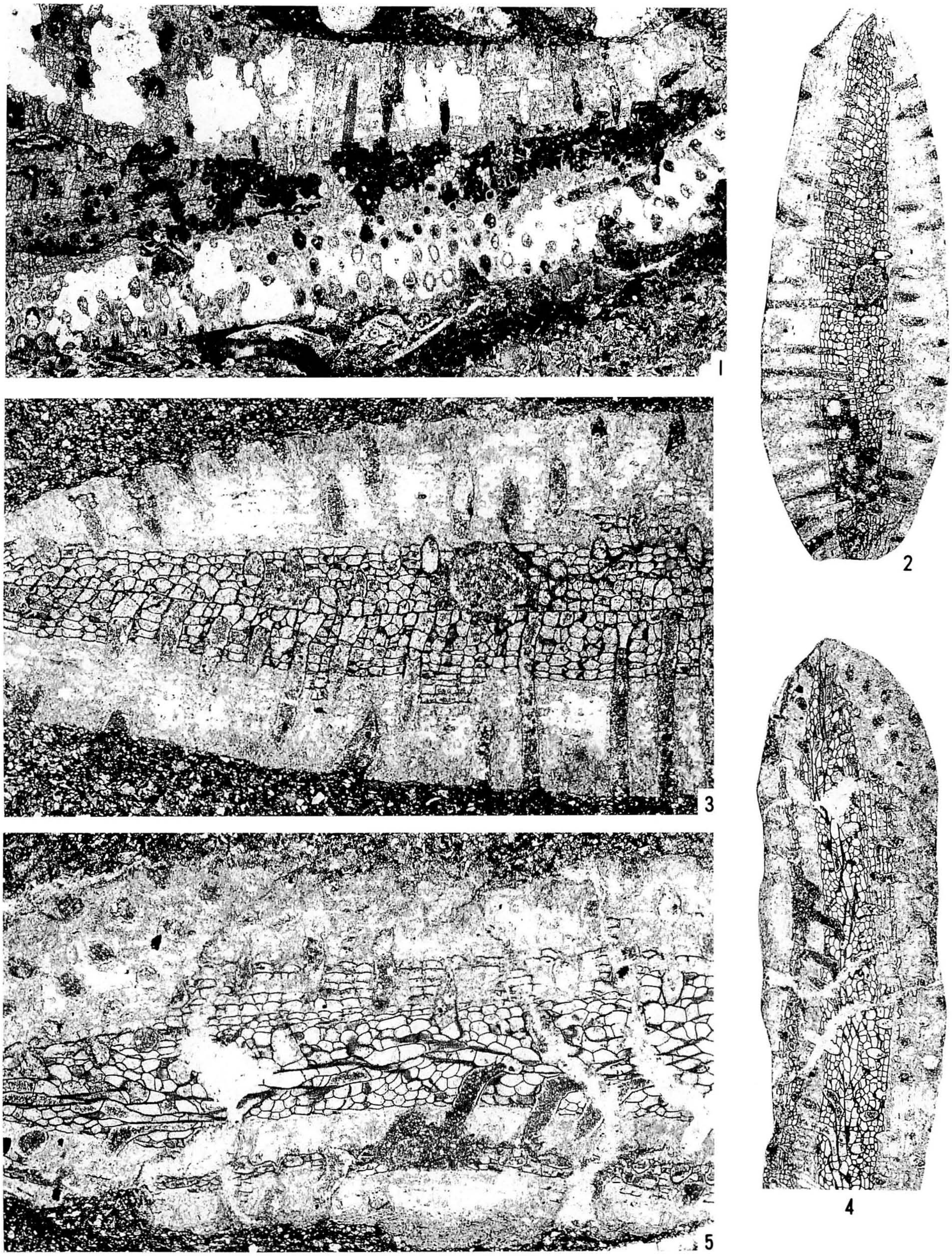

Figure 13. **1.** *Meekopora* sp. indet., longitudinal section, ×10, DESC-95067 (Ya39a-2). **2**-**5.** *Meekopora prosseri* Ulrich, 2, 4 : longitudinal sections, ×10, DESC-95205 (Cu115-16) and DESC-95203 (Cu115-11) respectively, 3, 5 : enlarged parts of 2 and 4, ×20.

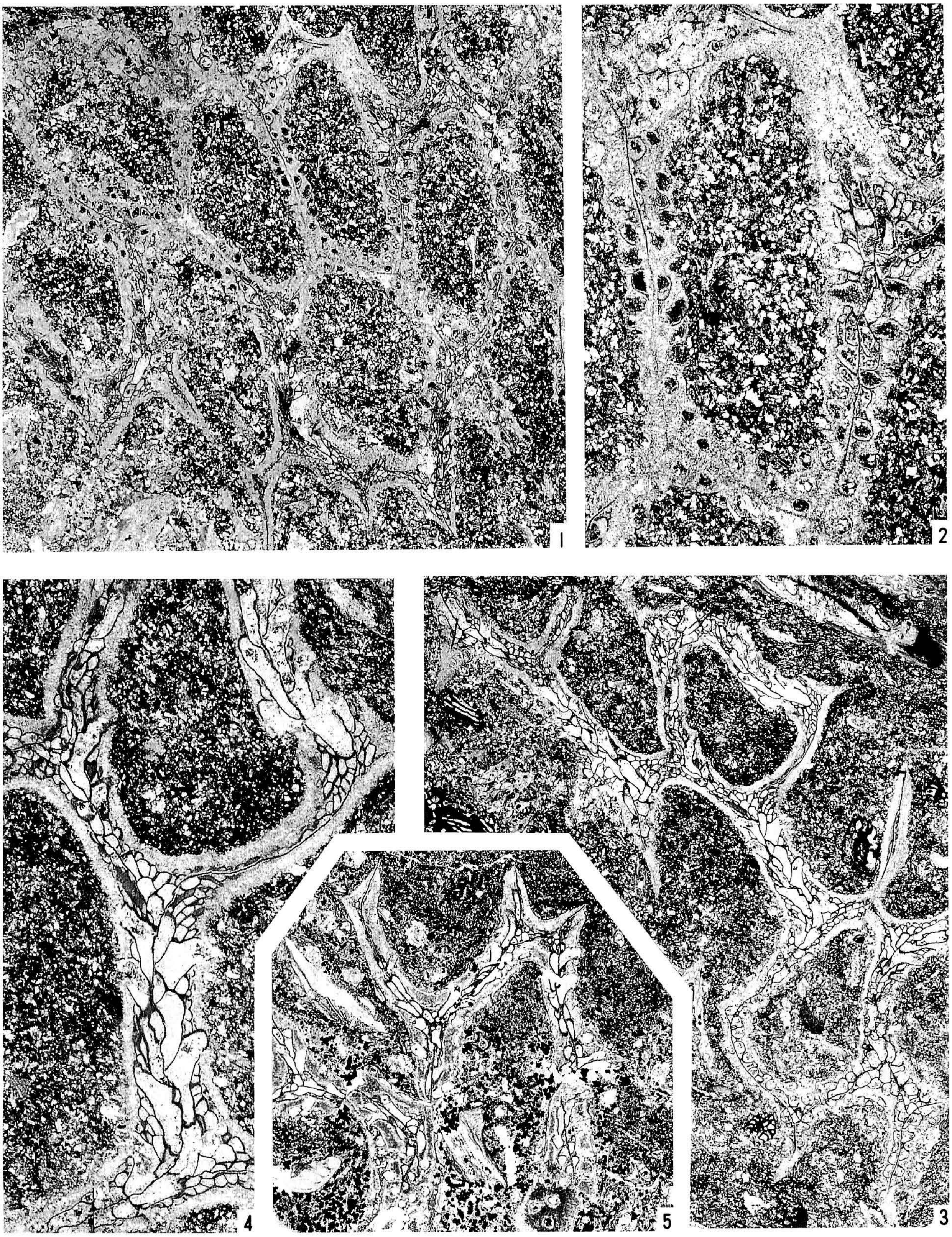

Figure 14. **1–5.** *Goniocladia peruviana* Chronic, 1, 3, 5 : tangential sections, ×10, DESC-95208 (Yp65-1), DESC-95188 (Cu114-21) and DESC-95014 (Ya12a-1), respectively, 2, 4 : enlarged parts of 1 and 3, ×20.

Meekopora sp. indet.

Figures 12-5, 6 ; 13-1

Material.—DESC-95067 (Ya39a-2), DESC-95068 (Ya39a-3), DESC-95079 (Ya44a (below)-1), DESC-95119 (An40-5).

Horizon.—Lower to middle part of *Eoparafusulina* zone in Yaurichambi-a and Ancoraimes routes.

Description.—Zoarium bifoliate, but exact mode of bifurcation not known because the specimens are only observed in thin section. Thickness of zoarium not determined.

In tangential section, zooecial tubes circular, diameter from 0.154 to 0.192 mm, usually 5 to 6 zooecia per 2 mm diagonally. Lunarium indistinct or absent. Vesicular tissue regularly arranged, usually 1 to 3 vesicles between adjacent zooecia in inner zone, and covered by secondary mineralization.

In longitudinal section, zooecial tubes proximally parallel to mesotheca for a short distance and curving rapidly upward, and meeting surface of zoarium at an angle of 90°. Vesicular material only in inner zone, with 10 vesicles per mm horizontally, and dense fibrous material in outer zone. Diaphragms usually 2 in inner zone, spaced at about 0.25 to 0.32 mm.

Remarks.—These poorly preserved specimens are not determinable to species.

Family Goniocladiidae Waagen and Pichl, 1885
Genus ***Goniocladia*** Etheridge, 1876

Goniocladia peruviana Chronic, 1949

Figures 14-1—5

Goniocladia peruviana Chronic in Newell *et al*., 1949, p. 135 ; Chronic in Newell *et al*., 1953, p. 128, 129, pl. 25, figs. 4-8c.

Material.—DESC-95014 (Ya12a-1), DESC-95208 (Yp65-1), DESC-95210 (Yp65-6), ?DESC-95001 (Ya06a(1)-1).

Horizon.—Upper part of *Triticites* zone to lower part of *Pseudoschwagerina* zone in Yaurichambi-a route and *Triticites* zone and middle part of *Pseudoschwagerina* zone in Yampupata route.

Description.—Zoarium consisting of anastomosing branches. Fenestrules typically hexagonal or irregularly polygonal with rounded corners. Width of fenestrule varies from 1.5 to 2.5 mm, and length ranges from 3.2 to 4.1 mm. Number of fenestrules in 10 mm along longer diameter 2 to 2.5 and a long shorter diameter about 4. Width of branch ranges from 0.8 to 1.1 mm. Probably 3 alternating parallel zooecial rows on each side of zoarial branch. Zooecial tubes circular in tangential section near surface, diameter ranging from 0.128 to 0.154 mm, parallel to coenelasma for a short distance and curved gradually upward, meeting outer zoarial surface at an angle of about 90°. Diaphragms absent. Interzooecial tissue consists of vesicles in inner zone and dark fibrous material from 0.25 to 0.30 mm thick in outer zone.

Remarks.—Although *Goniocladia peruviana* was originally described based on only surface features (Chronic in Newell *et al*., 1949), the present specimens are similar to Chronic's specimens from the Copacabana Group in Peru in the size of meshwork. As Chronic noted, this species seems to be similar to *Goniocladia timorensis* Bassler (1929) from the Permian of Timor Island, and also to *G. americana* Girty (1908) from the Guadalupian of U.S.A. Among the four specimens at hand, the specimen (DESC-95001 (Ya06(1)-01), obliquely oriented section) from the upper part of the *Triticites* zone in Yaurichambi-a route is questionably included in the species.

Order Trepostomata Ulrich, 1882
Family Stenoporidae Waagen and Wentzel, 1886
Genus ***Stenodiscus*** Crockford, 1945

Stenodiscus altiplana sp. nov.

Figures 15-1—3

Material.—Holotype : DESC-95140 (Ma30-31-10b) ; Paratypes : DESC-95049 (Ya35a-1b), DESC-95050 (Ya35a-2), DESC-95054 (Ya35b-1), DESC-95066 (Ya38a-7), DESC-95070 (Ya39a(2)-1), DESC-95071 (Ya39a(2)-2), DESC-95072 (Ya43a-1), DESC-95073 (Ya43a-2a, b), DESC-95074 (Ya43a-3), DESC-95075 (Ya43a-4), DESC-95077 (Ya46 (below)-2), DSEC-95078 (Ya46 (below)-3), DESC-95079 (Ya46 (below)-4), DESC-95080 (Ya46 (below)-5), DESC-95081 (Ya46 (below)-6), DESC-95106 (An36-1), DESC-95107 (An36-10), DESC-95111 (An36-14), DESC-95114 (An38-5), DESC-95115 (An38-7), DESC-95133 (Ma30-31-3), DESC-95134 (Ma30-31-4), DESC-95135 (Ma30-31-5), DESC-95136 (Ma30-31-6), DESC-95138 (Ma30-31-8), DESC-95139 (Ma30-31-9), DESC-95141 (Ma30-31-11a), DESC-95147 (Ma32-6), DESC-95148 (Ma32-7).

Horizon.—Lower part of *Eoparafusulina* zone in Yaurichambi-a, Ancoraimes and Matilde routes.

Description.—Zoarium thick, cylindrical ramose stem, 8 to 12 mm, but occasionally 14 to 15 mm in diameter. Branching mode of zoaria not observed in thin sections. Thickness of exozone variable, ranging from 0.5 to 3.0 mm, but reaches 4 to 5 mm in some cases.

In longitudinal section, zooecial tubes parallel to longitudinal direction in inner part, gradually curving outward in outer part of endozone, and rapidly bending at base of exozone. Zooecia open almost at right angles to the surface. Zooecial walls thin and slightly crenulate in endozone, and becoming rapidly thickened at base of

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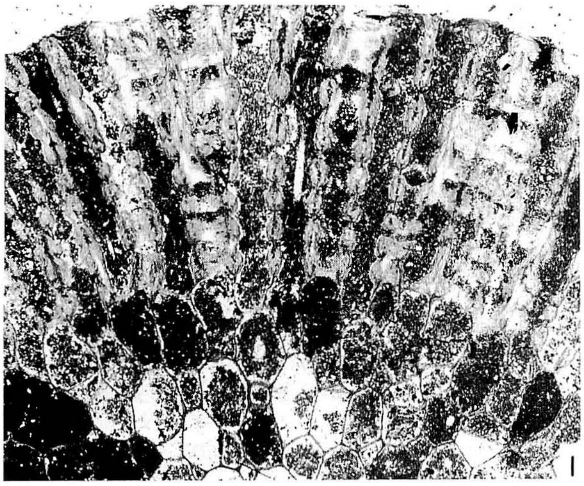
Figure 15. **1-3.** *Stenodiscus altiplana* sp. nov., 1, 2 : transverse and longitudinal sections, 3 : tangential section, ×20, paratype (DESC-95054 (Ya35b-1b)), holotype (DESC-95140 (Ma30-31-10b)) and paratype (DESC-95133 (Ma30-31-3)), respectively. **4.** *Rhombotrypella* ? sp. indet., transverse section, ×20, DESC-95006 (Ya07-2b). **5, 6.** *Rhombotrypella typica* (Bassler), longitudinal and tangential parts of the same zoarial section, ×20, DESC-95016 (Ya12a-3a).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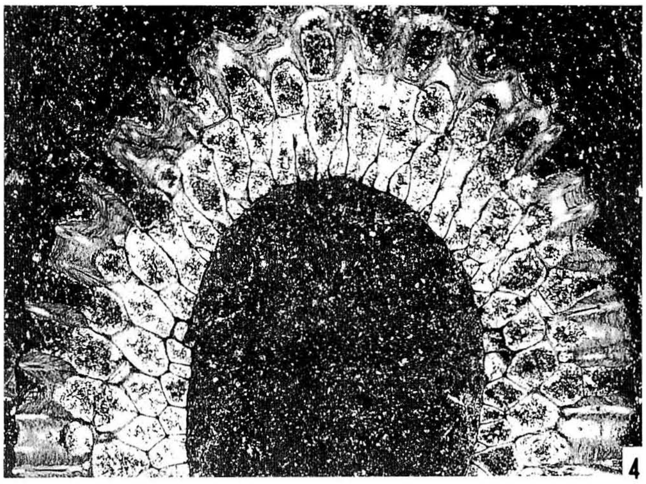
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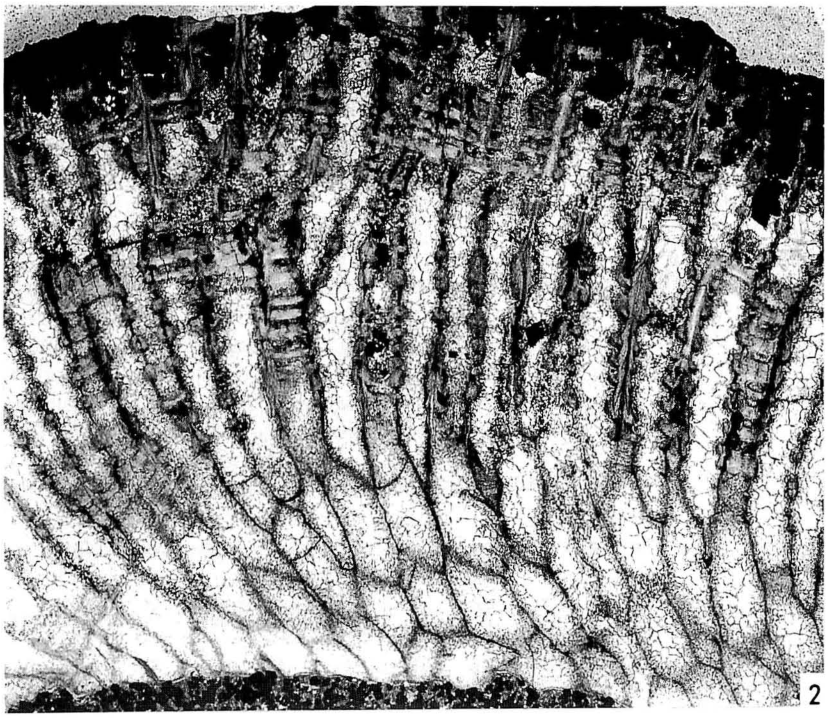
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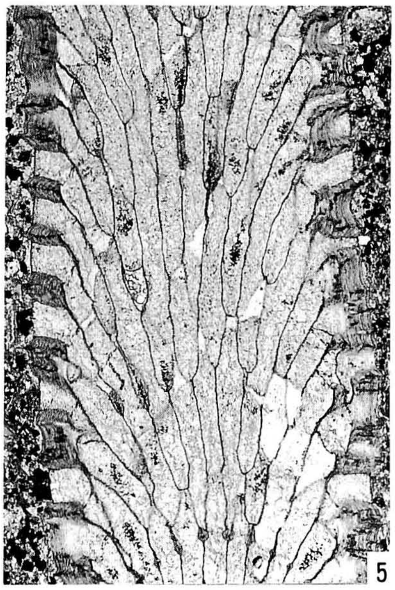
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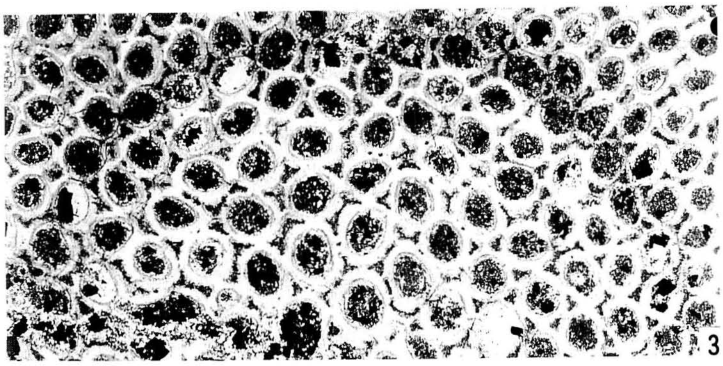
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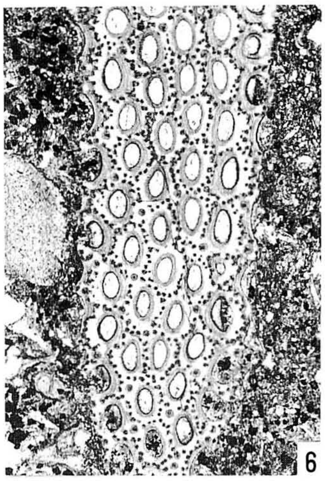
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mature exozone. This is composed of fine laminated fibrous tissue and is strongly moniliform. Individual monilae commonly short and closely strung together. Diaphragms usually absent but occasionally present in exozone and/or endozone tubes.

In a typical transverse section, zooecial tubes thin walled, irregularly arranged, polygonal in central part of endozone. Structures in exozone are the same as those in longitudinal section.

In tangential section, zooecia circular to oval and irregularly arranged, the longer diameter varies from 0.190 to 0.358 mm, and averages 0.260 mm; shorter diameter ranges from 0.141 to 0.256 mm, and averages 0.198 mm. Mesozooecia also circular to oval and very rare, diameter ranges from 0.064 to 0.128 mm, and averages 0.094 mm. Well developed acanthoecia having concentric laminate wall are usually located at the intersection of zooecial walls. Outside diameter ranges from 0.064 to 0.154 mm, and averages 0.104 mm.

Remarks.—This new species is closely similar to *Stenodiscus nicholsoni* (Waagen and Wentzel, 1886), originally described as a species of *Stenopora* from the Upper *Productus* Limestone. However, Waagen and Wentzel in their explanation of P1. CIX placed it in the Middle *Productus* Limestone from the mountain east of Katwahi, Pakistan. *S. nicholsoni* should be included in the genus *Stenodiscus* because the diaphragms are rarely present in the zooecial tubes. *S. altiplana* is distinguished from *S. nicholsoni* in having few mesozooecia which are common in *S. nicholsoni*.

Genus ***Rhombotrypella*** Nikiforova, 1933

Rhombotrypella typica (Bassler, 1936)

Figures 15-5, 6; 16-1—4

Rhomboporella typica Bassler, 1936, p. 159, 160, figs. 9-12.
non *Rhomboporella typica* Bassler. Shulga-Nesterenko, 1955, p. 98, pl. 13, figs. 7-9, text-fig. 8a.

Material.—DESC-95016 (Ya12a-3), DESC-95017 (Ya12a-4a), DESC-95018 (Ya12a-5), DESC-95031 (Ya12a-20b), DESC-95033 (Ya12a-26a), DESC-95049 (Ya35a-1a), DESC-95055 (Ya35c-2), DESC-95056 (Ya35c-3), DESC-95057 (Ya35c-4), DESC-95058 (Ya35c-5), DESC-95059 (Ya36a-1), DESC-95060 (Ya36a-2), DESC-95061 (Ya36a-3), DESC-95062 (Ya36a-4a, b), DESC-95082 (Ya47a-3), DESC-95083 (Ya47a-4), DESC-95084 (Ya47a-6a), DESC-95085 (Ya47a-8a), DESC-95088 (Yb20-1), DESC-95093 (Yc16-1b), DESC-95098 (Yc21a-2), IESC-95102 (Yc23a-a), DESC-95131 (Ma30-31-1a), DESC-95132 (Ma30-31-2a, b), DESC-95137 (Ma30-31-7a), DESC-95140 (Ma30-31-10a), DESC-95143 (Ma32-2b), DESC-95149 (Ma33-1), DESC-95150 (Ma33-3), DESC-95171 (Cu113-12), DESC-95200 (Cu115-5), DESC-95206 (Cu115-17), DESC-95213 (Yp65-9), DESC-95214 (Yp65-10b), DESC-95216 (Yp65-12b), DESC-95217 (Yp65-13a, b), DESC-95219 (Yp65-16a), DESC-95221 (Yp65-18b).

Horizon.—Lower part of *Pseudoschwagerina* zone to upper(?) part of *Eoparafusulina* zone in Yaurichambi-a, -b, and -c, Matilde, Cuyavi and Yampupata routes.

Description.—Zoarium cylindrical and ramose, branched at a wide angle, usually 2.5 to 4 mm diameter but varies from about 2 mm to 5.5 mm in zoarial diameter. Diameter of endozone also varying from 1.6 to 3.5 mm. Width of exozone narrow, usually less than 1 mm, ranging from 0.25 to 0.64 mm but reaching as much as 1.4 mm in part.

In longitudinal section, zooecial tubes straight, parallel to longitudinal direction in inner part of endozone and then rapidly curving outward at right angles at base of exozone. Zooecial walls thin and slightly crenulate in endozone, and showing progressive bifurcations which occur at definite curved levels across zoaria and become rapidly thickened, composed of finely laminated fibrous tissue in exozone. Monilae present but not prominent. Usually two kinds of diaphragms present in exozone of tube: one is a centrally perforated diaphragm at the base and another is a non-perforated, terminal diaphragm near zooecial opening.

In typical transverse section, zooecial tubes thin-walled, regularly arranged, quadrate in central part, and encompassed by a rhombic or polygonal pattern in outer part of endozone.

In tangential section, zooecia oval, regularly arranged in longitudinal and diagonal directions. 5 to 6, occasionally 7 zooecia per 2 mm longitudinally, and usually 7 per 2 mm diagonally. Longer and shorter diameters of zooecia range from 0.154 to 0.256 mm and 0.090 to 0.192 mm, respectively, and their average diameters 0.208 and 0.126 mm, respectively. Mesoecia rarely present, circular to oval, their shorter diameter ranges from 0.013 to 0.102 mm, and averages 0.062 mm. Megacanthoecia at the junctions of zooecial walls, composed of concentric fibrous calcite, their outside diameter ranges from 0.048 to 0096 mm, and averages 0.063 mm. Their inner diameter very small, probably less than 0.001 mm. Micracanthoecia in a single series between megacanthoecia, their outside diameter ranging from 0.020 to 0.032 mm.

Remarks.—The present species was originally described from the "Carboniferous" of Chulpapampa, Bolivia, which may correspond to the Copacabana Group. Bassler (1936) designated it as the type species of the genus *Rhomboporella* in the Order Cryptostomata. Subsequently, many researchers, such as Nikiforova (1939), Condra and Elias (1944), Shulga-Nesterenko (1955), Dunaeva (1956), Ross and Ross (1962), Małecki (1968), and Boardman and Mckinney (1976), have referred it to this genus. Boardman and Mckinney (1976) considered *Rhomboporella* a synonym of the genus *Rhombotrypella* Nikiforova (1939). In her systematic study of the Order Trepostomata, Astrova (1978) placed *Rhomboporella* Bassler in synonymy with *Rhombotrypella* Nikiforova.

This species is distributed widely in time and space in the Copacabana Group in the Lake Titicaca region. Bassler (1936) noted in his description of *Rhomboporella typica* that the zoarium diameter is 3 mm, however, it varies from 2 mm to 5.5 mm in the specimens at hand;

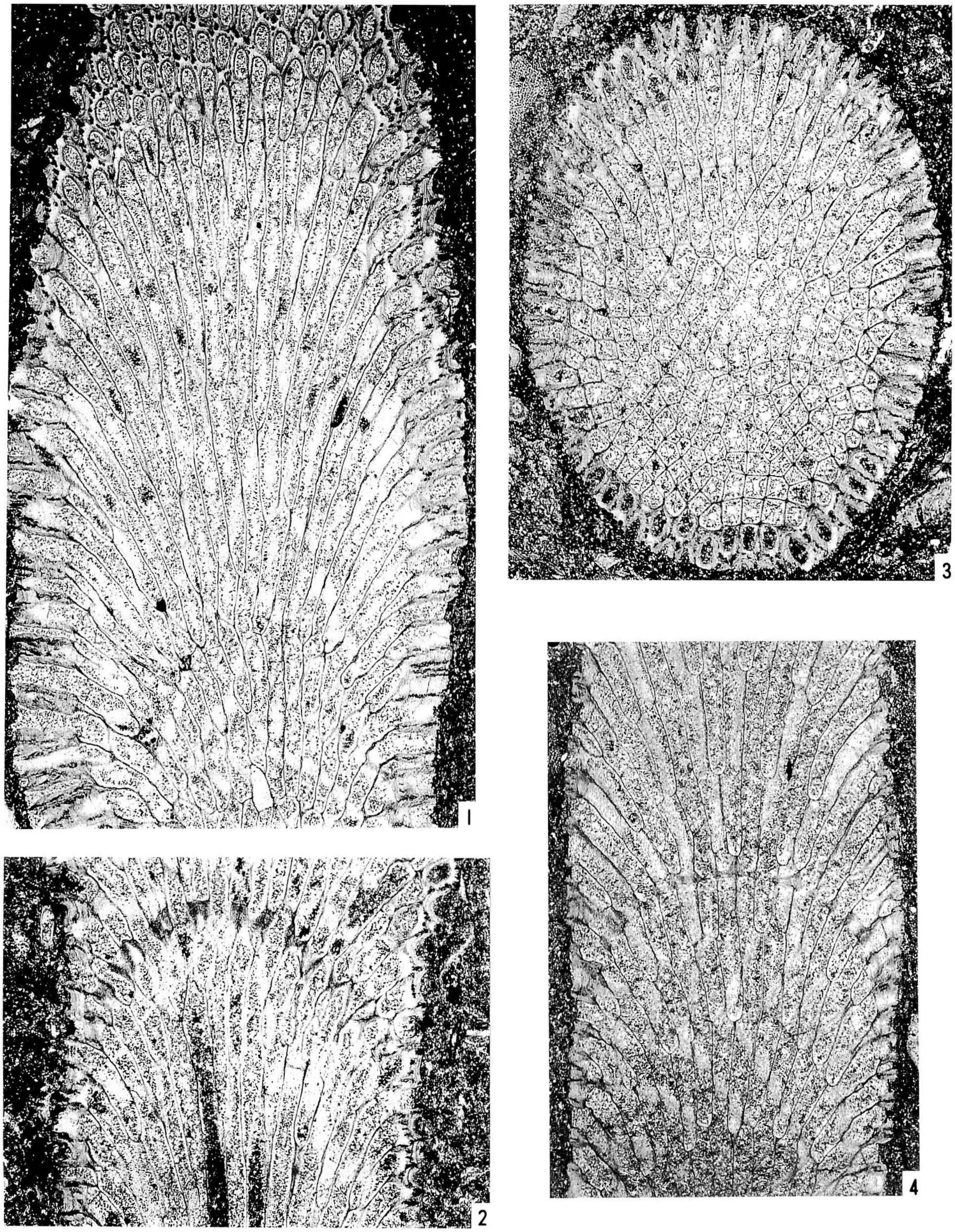


Figure 16. **1-4.** *Rhombotrypella typica* (Bassler), 1, 2, 4 : longitudinal sections, 3 : transverse section, × 20, DESC-95059 (Ya36a-1), DESC-95083 (Ya47a-8a), DESC-95062 (Ya36a-4b and 4a), respectively.

occasionally small branches (2 to 3 mm in diameter) arise from larger branches. Shulga-Nesterenko (1955) described material as *Rhomboporella typica* from the Gzhelian of the Late Carboniferous of Russian platform, but these specimens are distinguished from the Bolivian species by their thicker exozone.

The present species resembles *Rhombotrypella holmensis* Ross and Ross (1962) from the Desmoinesian (Pennsylvanian) of Northeast Greenland in most characters except for the difference in zoarial diameter as mentioned by them.

Rhombotrypella aff. ***R. gigantea*** Ross and Ross, 1962

Figure 17-6

Compared Rhombotrypella gigantea Ross and Ross, 1962, p. 27-29, pl. 6, figs. 2, 3, pl. 7, figs. 1, 3, 4, pl. 17, figs. 4, 5.

Rhombotrypella cf. *gigantea* Ross and Ross. Małecki, 1977?, p. 81, 82, pl. 4, figs. 1a-c.

Material.—DESC-95110 (An36-13).

Horizon.—Lower part of *Eoparafusulina* zone in Ancoraimes route.

Description.—A single longitudinal, partly tangential section shows a zoarium that is thick cylindrical and ramose ; about 8 mm in diameter. Diameter of endozone about 4 mm and width of exozone about 2 mm.

In longitudinal section, zooecial tubes parallel longitudinal direction, gradually curving outward in endozone, and straight and perpendicular to surface exozone. Zooecial walls thin and straight, with arcuate rows of monilae in endozone, and curving strongly outward at proximal end of exozone ; thickening rapidly and showing well developed monilae composed of finely laminated fibrous tissue in exozone. Perforated diaphragms usually lie between two monilae, as many as 6 per 2 mm length of tube.

In transverse section, zooecial tubes thin walled, regularly arranged quadrate or rhomboidal in central part.

In tangential section, zooecia circular to oval, irregularly arranged, longer diameter ranges from 0.154 to 0.256 mm, and averages 0.205 mm ; shorter diameter ranges from 0.128 to 0.179 mm, and averages 0.154 mm. Circular mesozooecia present but not numerous, diameter about 0.100 mm. Megacanthoecia located at intersections of zooecial walls and a single series of micracanthoecia arranged in outer part of zooecial walls. Outside diameters of megacanthoecia and micracanthoecia about 0.10 mm and 0.05 mm, respectively.

Remarks.—Although present in only one thin section, this fragment may be compared with *Rhombotrypella gigantea* Ross and Ross (1962) from the Wolfcampian ? of Northeast Greenland in the wide exozone, well developed monilae and numerous perforated diaphragms, as well as other characters. The zoarial diameter of the present form is a little smaller than that from Greenland, but this may not be so important for specific identification. Małecki (1977) described *Rhombotrypella* cf. *R. gigantea* from the upper Tokrossøya bed of Spitsbergen, and pointed out that the Spitsbergen specimen differed from the Greenland form in reduced zoarial dimensions and fewer perforated diaphragms.

Rhombotrypella ? sp. indet.

Figure 15-4

Material.—DESC-95005 (Ya07-1, DESC-95006 (Ya07-2b).

Horizon.—Upper part of *Triticites* zone in Yaurichambi-a route.

Description.—Zoarium is a cylindrical stem about 5 mm in diameter, having a hollow axial tube ; diameter of central hollow about 2.5 mm ; thickness of exozone 0.48 to 0.64 mm.

Zooecial walls thin in endozone and becoming rapidly thickened, composed of finely fibrous laminae in exozone. 2 or 3 centrally perforated diaphragms in exozone. No monilae present. Diameter of zooecia ranges from 0.230 to 0.256 mm, and averages 0.243 mm. No mesozooecia present. Megacanthoecia at junctions of zooecial walls, composed of concentric fibers, outside and inside diameters 0.080 to 0.096 mm and about 0.010 mm, respectively. Micracanthoecia probably arranged in a single series between megacanthoecia, outside and inside diameters less than 0.032 mm and 0.003 mm, respectively.

Remarks.—This form can be distinguished from *Rhombotrypella gigantea* by having a hollow axial zoarial epithecate tube. The specific identification is not made because of insufficient material comprising only two transverse sections.

Genus ***Tabulipora*** Young, 1883

Tabulipora cf. ***T. carbonaria*** (Worthen, 1875)

Figures 17-1—5

Chaetetes ? *carbonaria* Worthen in Worthen and Meek, 1875, p. 526, pl. XXXII, Fig. 5.

Stenopora carbonaria (Worthen). Ulrich, 1890, p. 445, pl. LXXIII, figs. 8-8a ; Condra, 1903, p. 45, 46, pl. 4, figs. 9-13 ; Condra and Elias, 1944, pl. 9, fig. 5.

Stenopora carbonaria var. *maculosa* Ulrich, 1890, p. 445, pl. LXXIII, figs. 10-10a.

Stenopora carbonaria var. *conferta* Ulrich, 1890, p. 446, p. LXXIII, figs. 9, 9a ; Condra, 1903, p. 46, pl. 4, figs. 14, 15.

Tabulipora carbonaria (Worthen). Cuffey, 1967, p. 1-96, pls. 1-9.

Tabulipora arcturusensis Gilmour, 1962, p. 1019, 1020, pl. 142, fig. 1-9.

Material.—DESC-95065 (Ya38a(up)-2a), DESC-95069 (Ya39a-6a), DESC-9569 (Ya39a-6b), DESC-95158 (Cu97-98-1), DESC-95159 (Cu97-98-2), DESC-95160 (Cu97-98-3).

Horizon.—Lower part of *Pseudoschwagerina* zone (*Omphalotrochus* horizon) in Cuyavi route, and middle part of *Eoparafusulina* zone in Yaurichambi-a route.

Description.—Zoarium cylindrical, ramose ; branching mode unknown, ranges from 6 to 9 mm in diameter. Diameter of endozone from 4.5 to 6 mm and width of

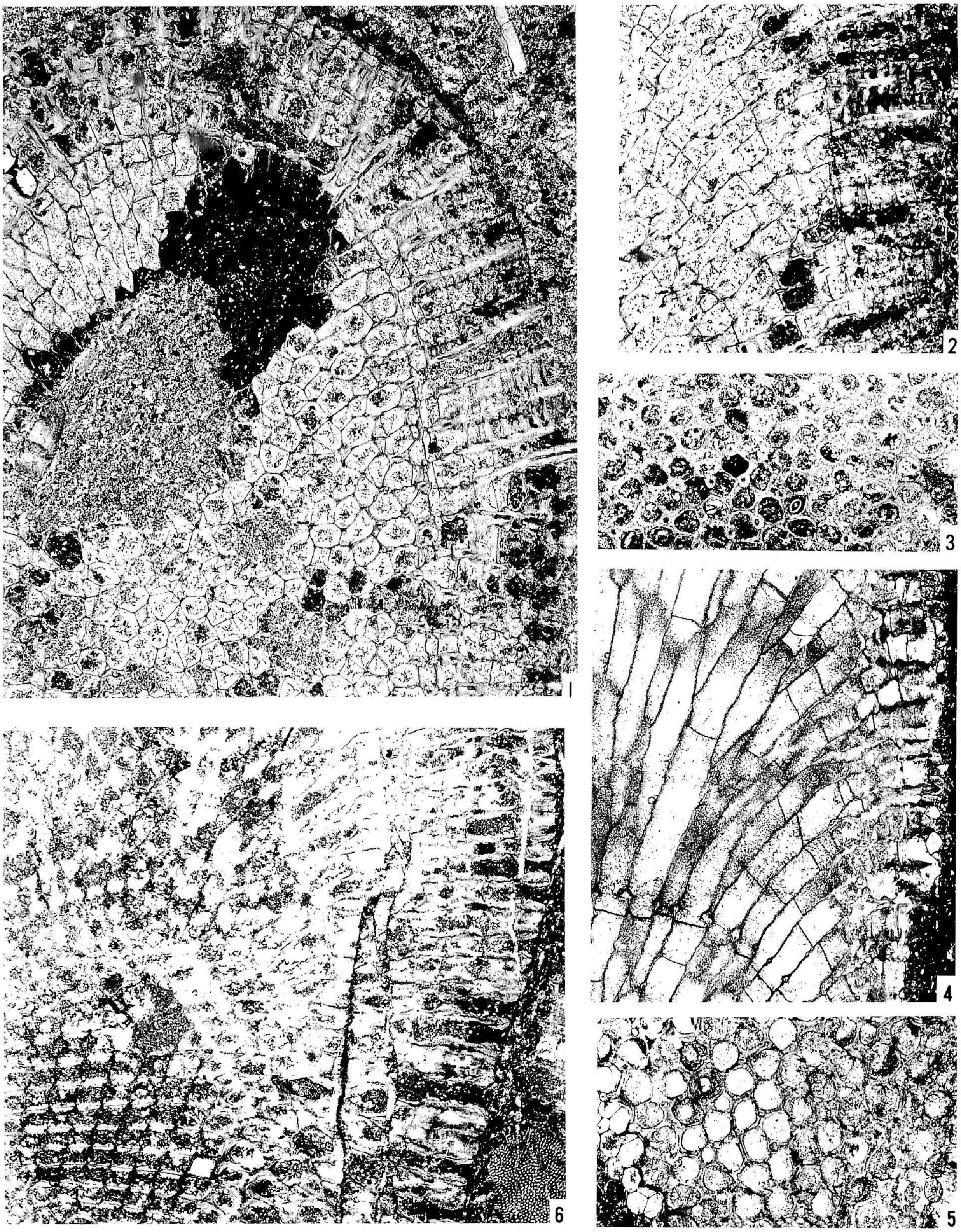


Figure 17. **1–5.** *Tabulipora* cf. *T. carbonaria* (Worthen), 1: transverse section, 2, 4: longitudinal sections, 3, 5: tangential sections, ×20, DESC-95065 (Ya38a(up)-2a), DESC-95069 (Ya39a-6a), DESC-95069 (Ya39a-6b), DESC-95160 (Cu97-98-3) and DESC-95158 (Cu97-98-1), respectively. **6.** *Rhombotrypella* aff. *R. gigantea* Ross and Ross, longitudinal section, ×20, DESC-95110 (An36-13).

exozone from 0.8 to 1.5 mm.

In longitudinal section, zooecial tubes parallel longitudinal direction in inner part and gradually curve outward in outer part of endozone, and are straight, perpendicular to surface in exozone. Zooecial walls thin, slightly crenulate, forming arcuate rows of monilae in endozone, and thickening rapidly with well developed monilae in exozone. Complete diaphragms at irregular intervals which generally shorten to outer part in endozone. In exozone of zooecial tubes, both complete and centrally perforated diaphragms at very short interspaces. Intervals between diaphragms vary from 0.13 to 0.32 mm in exozone. Inner edges of many of perforated diaphragms swollen and extending proximally.

In transverse section, zooecial tubes thin walled, irregularly arranged, polygonal in central part of endozone.

In tangential section, zooecia circular to polygonal with rounded corners and irregularly arranged, longer diameter ranges from 0.218 to 0.307 mm, and averaging 0.260 mm; shorter diameter ranging from 0.141 to 0.282 mm, and averaging 0.216 mm. Mesozooecia circular and rarely present, diameter ranges from 0.051 to 0.128 mm, and averaging 0.097 mm. Acanthoecia well developed, having dense laminate wall and usually located at junction of zooecial walls. Outside diameter of acanthoecia ranges from 0.080 to 0.128 mm, and averages 0.098 mm; and inner diameter large, 0.032 mm up to 0.045 mm. In some cases, very small granulated structure and/or divisional lines observed in central part of zooecial walls.

Remarks.—This species was described originally by Worthen (in Worthen and Meek, 1875), as a coral, *Chaetetes*, based only on the external colony. The internal structures were later examined and identified with the bryozoan genus *Stenopora* by Ulrich (1890). Easton (1943, p. 142) placed this species in the genus *Tabulipora*. A detailed study of *Tabulipora carbonaria* from the Wreford Megacyclothem (Lower Permian in Kansas, U.S.A.) by Cuffey (1967) showed that *Tabulipora carbonaria* is morphologically a highly variable and long ranging species, extending from the Middle Pennsylvanian through Early Permian (he estimated it to have ranged approximately 25my). The present Andean form is closely similar to *Tabulipora carbonaria*, but Cuffey does not recognize any mesozooecia in *Tabulipora carbonaria* and believes that unusually small zooecia seen externally and in tangential sections are those of zooecia introduced into the zoarium wthin the exozone. However, in the present form, the zooecia and mesozooecia can be distinguished clearly by their diameters. Cuffey (1967) included the following three species in *Tabulipora carbonaria*: *Tabulipora amsdenesis* Perry and Gutschick (1959), *Tabulipora arcturusensis* Gilmour (1962) and *Stenopora pauca* Perkins and Perry (1962). However, only *T. arcturusensis* from the Arcturus Formation (Permian) of eastern Nevada, U.S.A., may be synonymous. Gilmour (1962) observed that *Tabulipora arcturusensis* occurs in association with a gastropod, *Omphalotrochus*, in Nevada, and this is notable paleogeographically.

Tabulipora sp. indet.

Figures 18-1—4

Material.—DESC-95051 (Ya35a-3), DESC-95094 (Yc16-3b), DESC-95096 (Yc16-5b), DESC-95175 (Cu113-16c, d), DESC-95177 (Cu113-18), DESC-95178 (Cu113-19), DESC-95179 (Cu113-24).

Horizon.—Upper part of *Pseudoschwagerina* zone in *Cuyavi route* and middle part of *Eoparafusulina* zone in Yaurichambi-a route.

Description.—Zoarium lamellate, occasionally multiply (3 to 4) layered, thickness of single layer ranges from about 1 to 3 mm. Thickness of exozone about 0.4 to 0.6 mm.

In longitudinal section, zooecial tubes proximally parallel to zoarial base, and then bending rapidly perpendicular to surface. Zooecial walls thin in endozone and rapidly thickened in exozone, and consisting of fine fibers. Monilae developed but not prominent. Centrally perforated diaphragms that usually appear in thin section, rare or irregularly distributed, at intervals usually ranging from 0. 320 to 0.640 mm.

In tangential section, zooecial tubes polygonal with thin zooecial walls in endozone; polygonal with rounded corners or circular, and thick walls in exozone. Prominent acanthoecia usually at the intersection of zooecial walls. Outside and inner diameters of acanthoecia range from 0.064 to 0.112 mm and 0.005 to 0.032 mm, respectively.

Remarks.—This lamellate *Tabulipora* is characterized by rare, centrally perforated diaphragms and poorly developed monilae. Moore (1929) described *Tabulipora plummeri*, an encrusting zoarium, from the Upper Graham Formation (Pennsylvanian) of north-central Texas, however, no detailed comparison could be made because there is no description or illustrations of the internal structures.

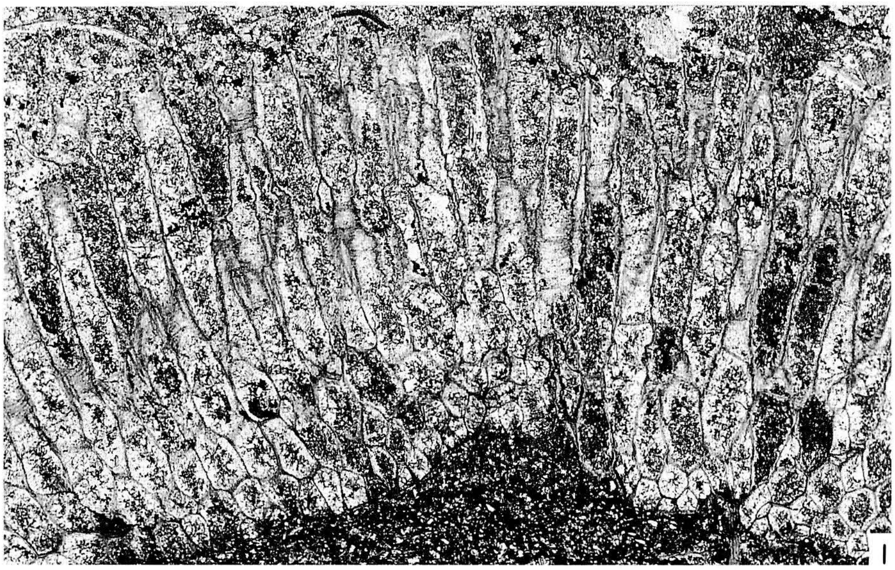
Family Dyscritellidae Dunaeva and Morozova, 1967
Genus **Dyscritella** Girty, 1911

Dyscritella tenuirama Crockford, 1957

Figures 18-5, 6

Dyscritella tenuirama Crockford, 1957, p. 52, 53, pl. 13, figs. 1, 2; Sakagami, 1968, p. 54, 55, pl. VIII, figs. 4-8.

Figure 18. 1-4. *Tabulipora* sp. indet., 1, 3, 4: longitudinal sections, 2: tangential section, ×20, DESC-95051 (Ya35a-3), DESC-95178 (Cu113-19), DESC-95177 (Cu113-18) and DESC-95179 (Cu113-24), respectively. **5, 6.** *Dyscritella tenuirama* Crockford, obliquely longitudinal and transverse sections, ×20, DESC-95090 (Yb20 (block)-4a) and DESC-95088 (Yb20 (block)-3), respectively. **7, 8.** *Dyscritella* aff. *D. komukensis* Sakagami, obliquely transverse and longitudinal sections, ×20, DESC-95145 (Ma32-4b) and DESC-95146 (Ma32-5b), respectively.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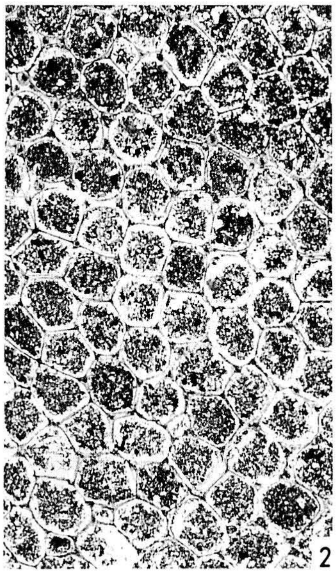
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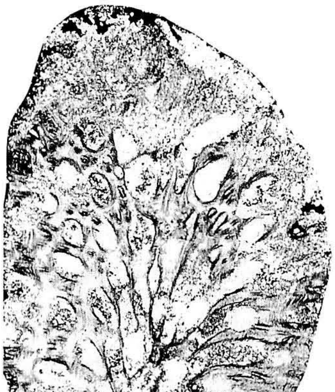
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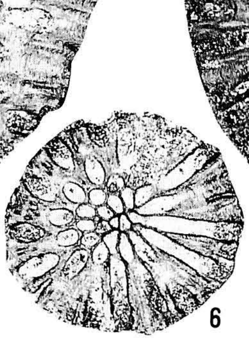
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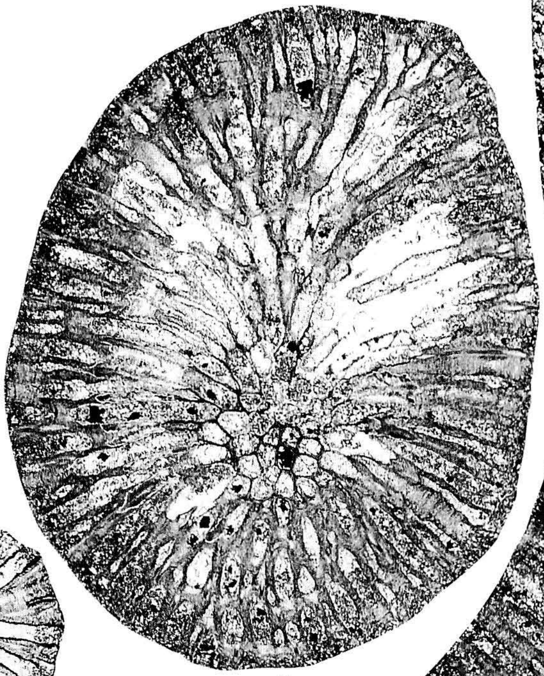
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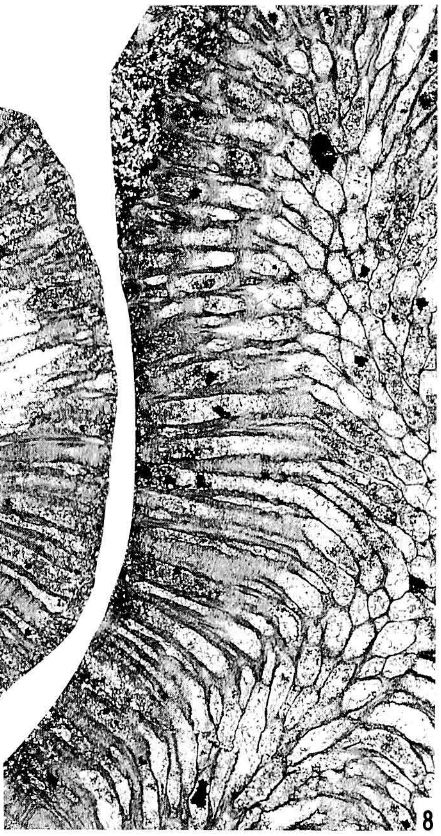
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Dyscritella cf. *tenuirama* Crockford. Sakagami, 1970, p. 50, 51, pl. VII, fig. 7.

Material.—DESC-95085 (Ya47a-8b, c), DESC-95089 (Yb20(block)-3), DESC-95090 (Yb20(block)-4a, b), DESC-95091 (Yb20(block)-5a, b, c), DESC-95229 (Yp92(up)-1a, b), DESC-95230 (Yp92(up)-3), DESC-95231 (Yp92(up)-6), DESC-95117 (An39-2c, d).

Horizon.—Lower to middle part of *Eoparafusulina* zone in Yaurichambi-a and -b, Yampupata and Ancoraimes routes.

Description.—Zoarium slender, cylindrical ramose branches, diameter ranges from 1.3 to 2.5 mm, averaging ca. 1.7 mm measured on 15 specimens. No surface specimens were obtained, but observation of a tangential section near the surface suggests that zooecial apertures probably are regularly arranged longitudinally and diagonally. Number of zooecial apertures about 3 in 1 mm longitudinally and 4 in 1 mm diagonally.

In longitudinal section, zooecial tubes parallel longitudinal direction of zoarium in inner part of endozone, but gradually curve outward to meet outer surface of zoarium at an angle of 90°. Zooecial walls straight, thin with a central black line in endozone, and becoming rapidly thickened with finely laminated fibers in exozone. Length of mature tubes ranges from 0.32 to 0.60 mm, averaging 0.45 mm measured on 14 specimens. Diaphragms absent.

In transverse section, zooecial tubes thin walled, polygonal in central part of endozone.

In tangential section near the surface, zooecial tubes oval, longer diameter ranges from 0.179 to 0.256 mm, averaging 0.186 mm measured on 9 specimens; shorter diameter ranges from 0.090 to 0.154 mm, averaging 0.121 mm measured on 16 specimens. Mesozooecia oval and sporadic, 0.026 to 0.077 mm, averaging 0.044 mm measured on 9 specimens. Well developed acanthoecia usually located at intersection of zooecial walls in inner part of exozone, increasing in number in outer part. Outside diameter ranges from 0.026 to 0.064 mm, averaging 0.048 mm on 7 specimens; inner diameter ranges from 0.003 to 0.010 mm, averaging 0.007 mm on the same 7 specimens.

Remarks.—The present form is closely similar to the specimens described from the Noonkanbah and Liveringa Formations of the Fitzroy basin, Western Australia. *Dyscritella tenuirama* has been reported also from the Permian of the peninsular part of Thailand; one occurrence is from Khao Ta Mong Rai, considered to be Artinskian or Leonardian in age, and another comparable form from Ko Muk, is considered to be Late Artinskian to Late Kungurian in age.

Dyscritella **aff.** ***D. komukensis*** Sakagami, 1970

Figures 18-7, 8

Compared Dyscritella komukensis Sakagami, 1970, p. 49-51, pl. XIII, figs. 1-5.

Material.—DESC-95142 (Ma32-1b), DESC-95145 (Ma32-4b), DESC-95146 (Ma32-5b).

Horizon.—Lower part of *Eoparafusulina* zone in Matilde route.

Description.—Zoarium cylindrical, ramose branches, diameters 4.2 to 4.3 mm measured on 3 specimens. Based on a tangential section near the surface zooecial apertures do not show any special regularity in either longitudinal or diagonal direction.

In longitudinal section, zooecial tubes parallel to longitudinal direction of zoarium in endozone and bending gradually outward, but curving rapidly at the boundary between immature and mature tubes so as to meet outer surface of zoarium at an angle of about 90°. Mature tubes straight and long, ranging from 1.2 to 1.6 mm, averaging 1.4 mm on 3 specimens. Zooecial walls thin and nearly straight in endozone, but rapidly thickened and consisting of laminated fibers in exozone. Diaphragms lacking.

In transverse section, zooecial tube thin walled, irregularly arranged polygons in central part of endozone.

In tangential section, zooecia circular to oval and irregularly arranged; larger diameter ranges from 0.128 to 0.218 mm, averaging 0.186 mm measured on 2 specimens; shorter diameter ranges from 0.102 to 0.154 mm, averaging 0.136 mm on 3 specimens. Mesozooecia very common, circular but occasionally irregularly shaped and variable in size ranging from 0.026 to 0.077 mm. Acanthoecia present but not prominent, surrounded by concentric dark dense fibers, outside and inner diameters ranging from 0.032 to 0.050 mm and 0.003 to 0.005 mm, respectively.

Remarks.—The present form is identical with *Dyscritella komukensis* Sakagami (1970), described from the Lower Permian of Ko Muk, the peninsular part of Thailand, in all characters and measurements except for the larger zoarium diameter.

Genus ***Pseudobatostomella*** Morozova, 1960

Pseudobatostomella micropora sp. nov.

Figures 19-1—4

Material.—Holotype: DESC-95045 (Ya33b-8b); Paratypes: DESC-95041 (Ya32c-3a, b), DESC-95042 (Ya32c-4), DESC-95043 (Ya33b-4a), ?DESC-95063 (Ya36a'-2a), DESC-95064 (Ya38a(up)-1a, b), DESC-95065 (Ya38a(up)-2b), DESC-95092 (Yb24b-2), DESC-95103 (Yc25-1).

Horizon.—Lower to middle part of *Eoparafusulina* zone in Yaurichambi-a, -b and -c routes.

Description.—Zoarium cylindrical ramose branches, diameter ranges from 1.1 to 3.2 mm, averaging 1.8 mm on 10 specimens. A tangential section near the surface suggests zooecial apertures do not show any special alignment in either longitudinal or diagonal direction.

In longitudinal section, zooecial tubes parallel to longitudinal direction of zoarium in endozone, but curve gradually outward to be at an angle of about 90° to outer surface of zoarium. Length of mature tubes short, ranging from

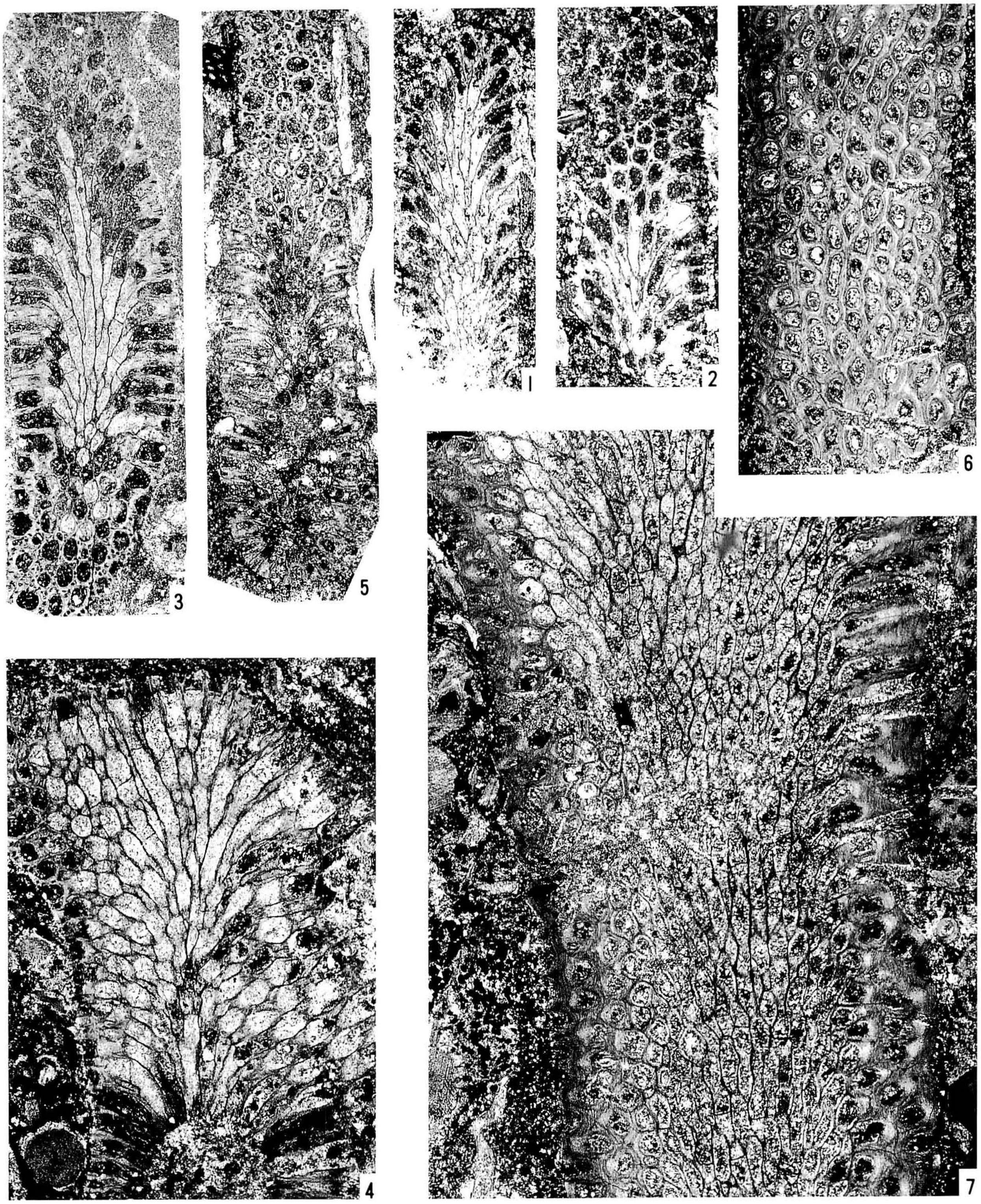

Figure 19. 1-4. *Pseudobatostomella micropora* sp. nov., longitudinal sections, ×20, paratypes (DESC-95041 (Ya32c-3a and 3b)), holotype (DESC-95045 (Ya33b-8b)) and paratype (questionably referred, DESC-95063 (Ya36a′-2a)), respectively. **5.** *Pseudobatostomella* sp. indet., longitudinal but partly tangential section, ×20, DESC-95151 (Ma35 (below)-1). **6, 7.** *Pseudobatostomella yanagidai* sp. nov., tangential and longitudinal parts of the same zoarial section, ×20, holotype (DESC-95108 (An36-11)).

0.25 to 0.64 mm, averaging 0.39 mm on 10 specimens. Zooecial walls thin and slightly crenulate in endozone, then rapidly thickened and consisting of finely laminated fibers in exozone. Usually 2 to 3 straight or slightly concave diaphragms at irregular intervals in immature tubes, and only one diaphragm, although partly absent, in middle part of mature tube.

In transverse section, zooecial tubes thin-walled, irregularly arranged polygons in central part of endozone.

In tangential section near the surface, zooecial tubes elongated circular to oval and irregularly arranged ; longer diameter ranges from 0.141 to 0.256 mm, averaging 0.212 mm on 8 specimens ; shorter diameter ranges from 0.102 to 0.179 mm, averaging 0.131 mm on 10 specimens. Mesozooecia sporadic and the diameters vary from 0.026 to 0.077 mm, averaging 0.054 mm on 8 specimens. Well developed acanthoecia surrounded by concentric laminate wall, located usually at the intersection of zooecial walls but occasionally at an intermediate point between them ; outside diameter ranges from 0.026 to 0.048 mm, averaging 0.036 mm on 9 specimens ; and inner diameter large, ranges from 0.005 to 0.006 mm.

Remarks.—This new species is not unlike *Pseudobatostomella spinigera* (Bassler, 1929) and *P. cylindrica* (Crockford, 1941), both of which were described as *Batostomella*, but it can be distinguished from these two species by the smaller diameter of the zooecial tube and the presence of diaphragms in the immature tube.

Pseudobatostomella yanagidai sp. nov.

Figures 19-6, 7

Material.—Holotype : DESC-95108 (An36-11) ; Paratypes : DESC-95109 (An36-12), ?DESC-95044 (Ya33b-6a).

Horizon.—Lower part of *Eoparafusulina* zone in Ancoraimes route and questionably in Yaurichambi-a route.

Description.—Zoarium cylindrical ramose branches, but branching pattern is unknown ; ranges from 3.3 to 3.9 mm in diameter. A tangential section near the surface shows no special pattern in either longitudinal or diagonal direction. Diameter of endozone ranges from 2.3 to 2.5 mm and width of exozone ranges from 0.8 to 1.0 mm.

In longitudinal section, zooecial tubes parallel to longitudinal direction in inner part, rather rapidly curved outward at the boundary between immature and mature tubes, and straight and perpendicular to the surface in exozone. Zooecial walls thin, slightly crenulate in endozone, and rapidly thickened, consisting of coarse fibers in exozone. Complete diaphragms rare in immature tubes and absent in mature tubes.

In transverse section, zooecial tubes thin-walled, irregularly arranged polygons in central part of endozone.

In tangential section, zooecial tubes circular or rhomboidal with rounded corners but occasionally irregularly shaped ; longer diameter ranges from 0.179 to 0.218 mm, averaging 0.199 mm ; shorter diameter ranges from 0.102 to 0.141 mm, averaging 0.122 mm. Mesozooecia rare, rounded triangular to oval, shorter diameter ranging from 0.038 to 0.064 mm, averaging 0.051 mm. Acanthoecia poorly developed, usually located at the junction of zooecial walls. Outside and inner diameters about 0.032 mm and 0.006 to 0.010 mm, respectively. A whitish but occasionally blackish divisional line observed in central part of zooecial walls.

Remarks.—This species is characterized by the relatively large diameter of the zoarium, rare diaphragm only in the immature tube and poorly developed acanthoecia near the surface. This species is comparable with neither any of the species listed by Astrova (1978) nor other described species. The specific name is dedicated to Professor Juichi Yanagida of Kyushu University, who has always kindly helped me, not only in field surveys but also in laboratory work.

Pseudobatostomella sp. indet.

Figure 19-5

Material.—DESC-95151 (Ma35(below)-1), DESC-95152 (Ma37(20 cm, below)-2c).

Horizon.—Lower part of *Eoparafusulina* zone in Matilde route.

Description.—Zoarium cylindrical ramose branches, diameter 1.0 to 1.3 mm ; a tangential section near the surface shows that zooecial apertures do not show any special pattern in longitudinal or diagonal direction.

In longitudinal section, zooecial tubes parallel to longitudinal direction of zoarium in endozone, but curved gradually outward and outer surface of zoarium at an angle of about 90°. Zooecial walls thin and slightly crenulate in endozone, rapidly thickened and consisting of finely laminated fibers in exozone. Length of mature tubes ranging from 0.32 to 0.38 mm. Usually one straight diaphragm located at boundary between mature and immature parts of tube.

In transverse section, zooecial tubes thin-walled, irregularly arranged polygons in central part of endozone.

In tangential section near the surface, zooecial tubes circular to oval in shape and irregularly arranged ; longer and shorter diameters range from 0.154 to 0.179 mm and 0.090 to 0.141 mm, respectively. Small mesozooecia commonly present ; diameters range from 0.026 to 0.051 mm. Many acanthoecia surrounded by concentric laminate walls, lie usually at each point of intersection of a zooecial tube and 5 to 8 surround each zooecial aperture. Outside and inner diameters range from 0.026 to 0.048 mm and 0.003 to 0.005 mm, respectively.

Remarks.—The present form seems to differ from *Pseudobatostomella micropora* sp. nov. by a larger number of acanthoecia. The specific identification, however, must be postponed until more specimens are available.

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998 Upper Paleozoic bryozoans from the Lake Titicaca region, Bolivia
Part 2. Systematic paleontology

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Abstract. Part of the systematic paleontology of Upper Paleozoic bryozoans from the Lake Titicaca region is found in Part 1 of the present article, Part 2 describes two remaining orders, Cryptostomata and Fenestrata. Two new species, *Rhombopora kawabei* and *Septopora andeana*, are proposed in the families Rhomboporidae and Septoporidae, respectively.

Key words : Bryozoans, biostratigraphy, Copacabana Group, Lake Titicaca region (Bolivia), Upper Paleozoic

Introduction

This article is the second installment of a study of Upper Paleozoic bryozoans from the Lake Titicaca region, Bolivia, and gives systematic descriptions of two orders, Cryptostomata and Fenestrata. Of the four orders of bryozoans recognized in the Bolivian Upper Paleozoic bryozoan fauna, two orders, Cystoporata and Trepostomata, were described in Part 1 of the present article.

Systematic paleontology

Order Cryptostomata Vine, 1883
Suborder Rhabdomesina Astrova and Morozova, 1956
Family Rhomboporidae Simpson, 1895
Genus **Rhombopora** Meek, 1872

Rhombopora lepidodendroides Meek, 1872

Figures 1-1—6

Rhombopora lepidodendroides Meek. Newton, 1971, p. 28, 29, 31-35, pl. 1, figs. 1-6, 11, 12, pl. 2, figs. 1-8, 11, 16 (see the synonym list).

Material.—DESC-95002 (Ya06a (2)-1a), DESC-95003 (Ya06a (2)-2), DESC-95004 (Ya06a(2)-3a, b), DESC-95021 (Ya12a-8a, b), DESC-95034 (Ya20a-3), DESC-95086 (Yb10a-1), DESC-95096 (Yc16-5), DESC-95097 (Yc16-6), DESC-95105 (An22-4), DESC-95122 (An48-4a, b), DESC-95174 (Cu113-15a).

Horizon.—Upper part of *Triticites* zone to upper part of *Pseudoschwagerina* zone at Yaurichambi-a route, upper part of *Triticites* zone at Yaurichambi-b route, upper part of *Pseudoschwagerina* zone at Yaurichambi-c route, and middle part of *Pseudoschwagerina* zone to middle part of *Eoparafusulina* zone at Ancoraimes route.

Description.—Zoarium consists of cylindrical stem, having small diameter, ranging from 1.0 to 1.6 mm among 14 specimens.

In longitudinal section, axial region formed by a nearly straight axis ; zooecial tubes straight, making a small angle with longitudinal direction in endozone, but rapidly bending outward at posterior end of tubes in exozone. Diameter of endozone varies from 0.5 to 1.1 mm. Thickness of exozone ranges from 0.25 to 0.48 mm.

In tangential section of exozone, zooecial tubes oval, longer diameter ranges from 0.167 to 0.320 mm, shorter diameter ranges from 0.115 to 0.192 mm ; arranged regularly longitudinally and diagonally, 3 to 4 zooecia per 2 mm longitudinally. Zooecial wall thin in endozone, but sharply thickened in exozone. One or 2 acanthostyles surrounded by concentric dark fibers ; outside diameter 0.040 to 0.080 mm. One row of paurostyles between acanthostyles ; outside diameter 0.020 to 0.032 mm. Inside diameter of acanthostyles and paurostyles is not measurable because they are too small.

Remarks.—Newton (1971) discussed in detail rhabdomesid bryozoans from the Wreford Megacyclothem (Wolfcampian, Permian) of the Midcontinental U.S.A. especially *Rhombopora lepidodendroides* which is most abundant in the Megacyclothem. He concluded that the total range of *R. lepidodendroides* was from the Early Pennsylvanian to Late Permian and that species varied little or not at all in its average morphologic features from Virgilian (Late Pennsylvanian) through Wreford (Early Permian) time, and that the geographic and stratigraphic variations of this species lacked any systematic pattern. The present form appears to be identical with *R. lepidodendroides* redefined by Newton in its essential characters, but there are some variations in the zoarial and zooecial diameters of the Titicaca specimens.

Rhombopora corticata Moore, 1929

Figures 1-7, 8 ; 2-1, 2

Rhombopora corticata Moore, 1929, p. 137, pl. 17, figs. 3, 4 ; text-figs. 4i, j.

Material.—DESC-95023 (Ya12a-10), DESC-95031 (Ya12a-20a), DESC-95104 (Yt01-3), DESC-95154 (Cu82-1), DESC-95155 (Cu82-2), DESC-95156 (Cu82-3), DESC-95157 (Cu82-4), DESC-95162 (Cu103-2), DESC-95180 (Cu114-2), DESC-95181 (Cu114-39, DESC-95183 (Cu114-5), DESC-95185 (Cu114-7), DESC-95186 (Cu114-8).

Horizon.—Lower part of *Pseudoschwagerina* zone at Yaurichambi-a and Yaurichambi-Yt routes, and upper part of *Pseudoschwagerina* zone at Cuyavi route.

Description.—Zoarium consisting of cylindrical stem ; diameter varies from 1.1 to 2.6 mm among 12 specimens.

In longitudinal section, axial region has irregularly linear axis and straight zooecial tubes, making a small angle with longitudinal direction in endozone, bending rapidly outward at posterior end of tubes in exozone. Diameter of endozone ranges from 0.6 to 1.3 mm. Thickness of exozone varies from 0.2 to 0.8 mm.

In tangential section of exozone, zooecial tubes oval ; longer diameter ranges from 0.205 to 0.320 mm, shorter diameter ranges from 0.128 to 0.167 mm, regularly arranged in longitudinal and diagonal directions ; 3 to 4 zooecia per 2 mm longitudinally and 5 to 5.5 per 2 mm diagonally. Zooecial wall thin in endozone, but sharply thickened in exozone. One to 2 acanthostyles, surrounded by concentric dark fibers at each intersection of zooecial tubes ; outside diameter ranges from 0.064 to 0.096 mm. One row of paurostyles between acanthostyles ; outside diameter ranges from 0.032 to 0.064 mm. Inside diameter of neither acanthostyles nor paurostymes is measurable because they are too small.

Remarks.—The present form is assigned to *Rhombopora corticata* which Moore (1929) described from the Upper Graham Formation (Pennsylvanian) in north central Texas, U.S.A. *R. corticata* is distinguished from *R. lepidodendroides* by the thicker exozone and larger zooecial tube as noted by Moore.

Rhombopora kawabei sp. nov.

Figures 2-3—6

Material.—Holotype : DESC-95113 (An38-4a) ; Paratypes : DESC-95116 (An39-1), DESC-95117 (An39-2a, b), DESC-95118 (An39-3), DESC-95120 (An43-1a), DESC-95121 (An44-29).

Horizon.—Lower part of *Eoparafusulina* zone at Ancoraimes route.

Description.—Zoarium consists of cylindrical stem, varying from 1.8 to 3.2 mm in diameter as measured on 7 specimens.

In longitudinal section, axial region consists of a nearly straight axis and straight zooecial tubes, making a small angle with longitudinal direction in endozone, and rapidly bending outward at posterior end of tubes in exozone. Zooecial tube in exozone straight and perpendicular to surface. Diameter of endozone ranges from 0.7 to 1.7 mm and width of exozone ranges from 0.5 to 0.8 mm.

In tangential section of exozone, zooecial tubes oval, longer diameter ranges from 0.192 to 0.256 mm, shorter diameter ranges from 0.102 to 0.154 mm, regularly arranged in longitudinal and diagonal directions, usually 3.5 to 4 zooecia per 2 mm longitudinally and 5.5 to 6 zooecia per 2 mm diagonally. Zooecial wall thin in endozone, but sharply thickened in exozone. Usually one, occasionally two, acanthostyles at each corner of zooecial tube and surrounded by concentric fibers ; outside diameter ranges from 0.064 to 0.096 mm. Inner diameters of acanthostyles and paurostyles very small, and not measurable.

Remarks.—The present species may be distinguished from *Rhombopora lepidodendroides* by the larger diameter of the zoarium and wider exozone, and from *R. corticata* by the smaller diameter of the zooecial tubes in exozone.

This species is named after Mr. Tetsuya Kawabe of Chiba University for his kind assistance in the field, and collecting and preparing bryozoan specimens.

Family Hyphasmoporidae Vine, 1886
Genus ***Strebotrypa*** Vine, 1885

Streblotrypa sp. indet.

Figures 1-9, 10

Material.—DESC-95090 (Yb20 (block)-4c), DESC-95091 (Yb20 (block)-5d).

Horizon.—Upper part of *Pseudoschwagerina* zone at Yaurichambi-b route.

Description.—Only two thin sections of fragmentary specimens were examined. Zoarium slender, cylindrical ramose branches, diameter 0.8 mm and 0.9 mm, respec-

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Figure 1. **1, 2.** *Rhombopora lepidodendroides* Meek, longitudinal and transverse sections, ×20, DESC-95002 (Ya06(2)-1a) and DESC-95003 (Ya06(2)-2), respectively. **3-6** *Rhombopora lepidodendroides* Meek, 3, 5, 6 : longitudinal sections, 4 : transverse and oblique sections, ×20, DESC-95021 (Ya12a-8a, 8b and 8c), DESC-95105 (An22-4) and DESC-95174 (Cu113-15a), respectively. **7, 8.** *Rhombopora corticata* Moore, oblique and longitudinal sections, ×20, DESC-95023 (Ya12a-10) and DESC-95031 (Ya12a-20a), respectively. **9, 10.** *Streblotrypa* sp. indet., obliquely transverse and longitudinal sections, ×20, DESC-95091 (Yb20 (block)-5d) and DESC-95090 (Yb20 (block)-4c), respectively.


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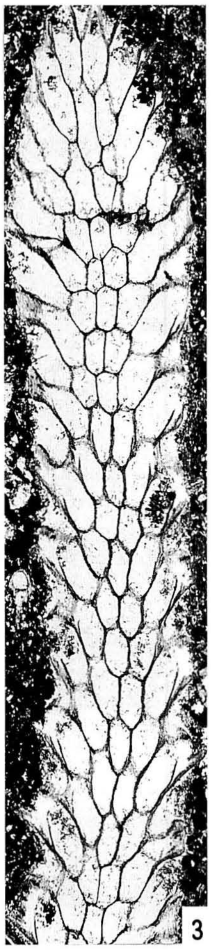
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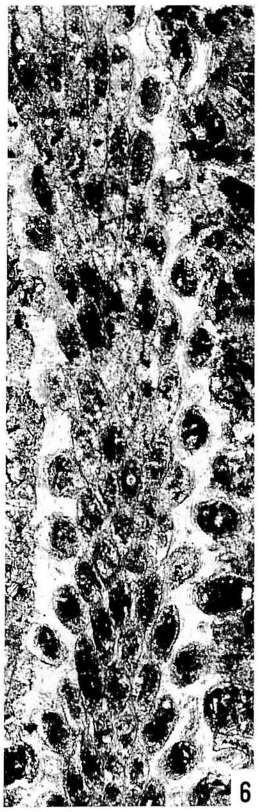
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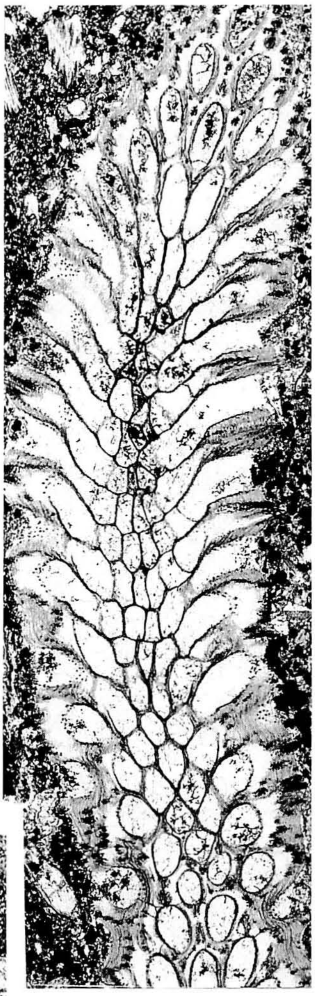


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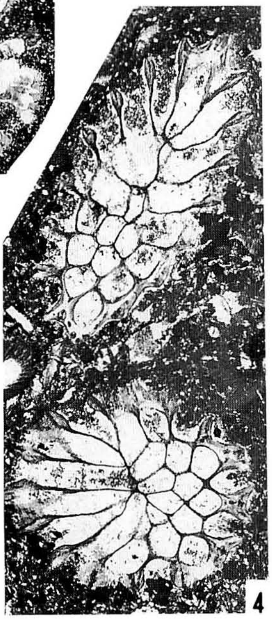
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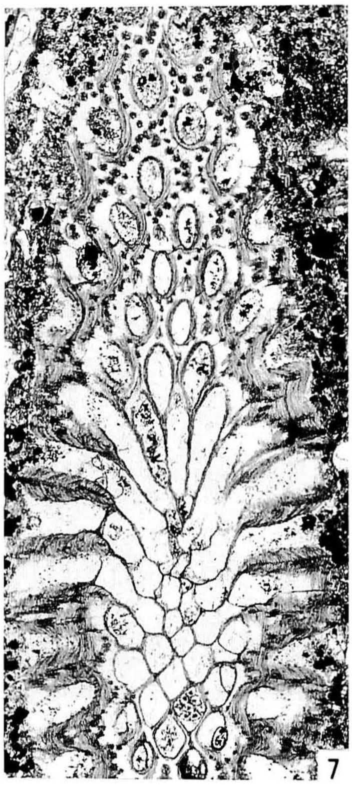
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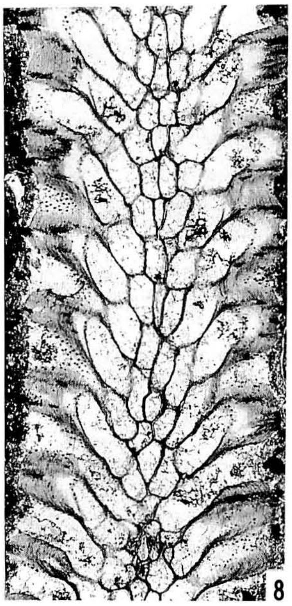
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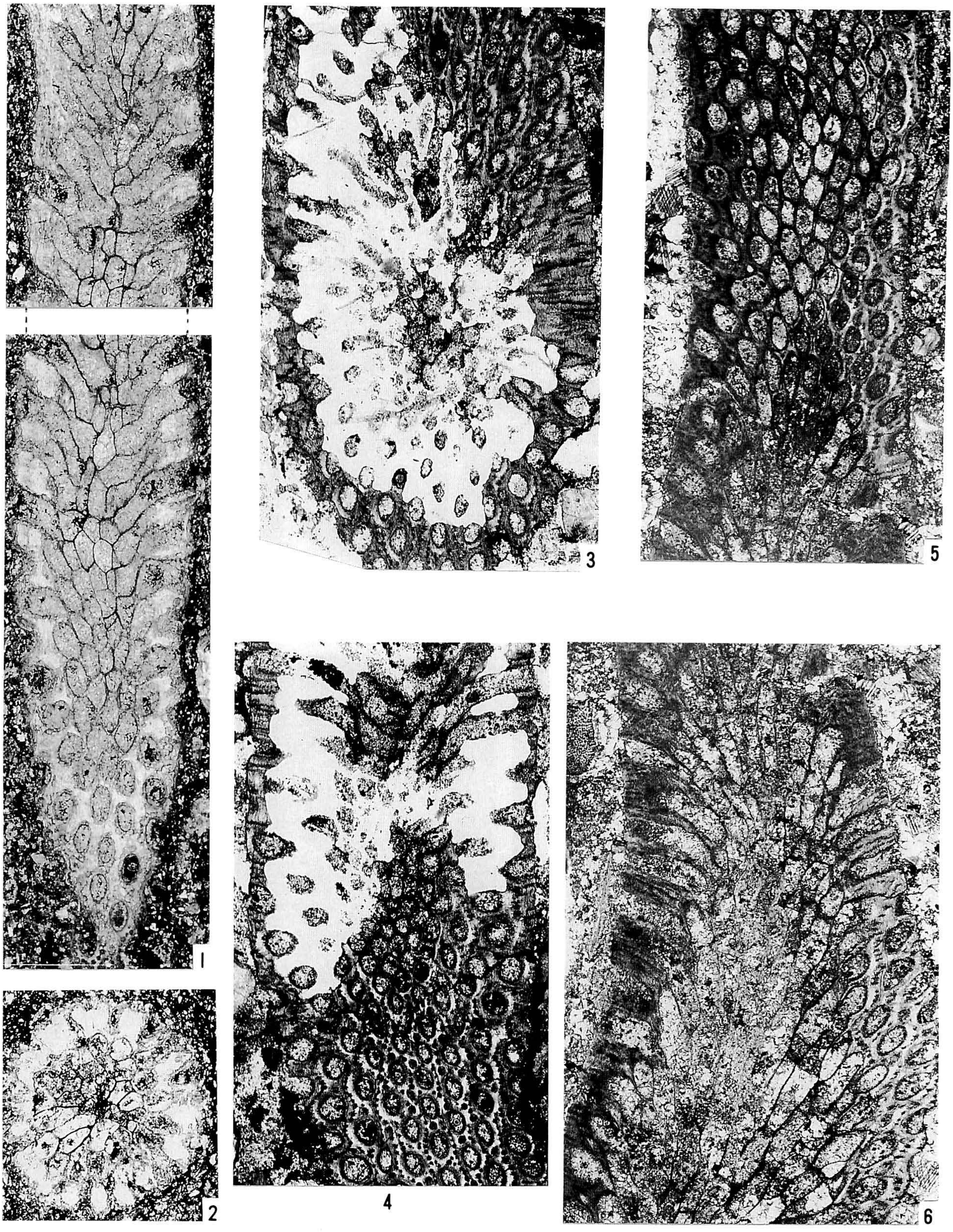


Figure 2. **1, 2.** *Rhombopora corticata* Moore, longitudinal and transverse sections, ×20, DESC-95181 (Cu114-3) and DESC-95183 (Cu114-5), respectively. **3-6**. *Rhombopora kawabei* sp. nov., longitudinal but partly tangential sections, ×20, paratypes (DESC-95117 (An39-2a), DESC-95116 (An39-1)), holotype (DESC-95113 (An38-4a (5, 6 are from the same zoarial section))), respectively.

tively.

In longitudinal section, diameter of central bundle 0.15 mm and 0.17 mm; number of tubes in central bundle usually 3. Ratios of zoarial diameter to central bundle about 5 : 1. Zooecial tubes arise from central bundle at an angle of about 20°, straight in endozone and curving rapidly at inner edge of exozone. Width of outer region of tube 0.13 mm and 0.18 mm. Metapores arise from base of exozone, approximately parallel to endozone wall for a very short distance, then curving rapidly outward and parallel to zooecial tubes in exozone.

In tangential section of exozone, zooecial tubes oval, longer diameter 0.115 to 0.141 mm and shorter diameter 0.090 to 0.102 mm, as measured on 2 specimens. Zooecial apertures arranged regularly in longitudinal and diagonal series. Superior hemiseptum at posterior end of exozone, inferior hemiseptum opposite side to superior hemiseptum. Usually two rows of metapores between zooecial tubes and 3 in each longitudinal row; total number of metapores usually 6. Diameter of metapore 0.026 to 0.032 mm. Diaphragms lacking. Because of lack of a true transverse section, number of tubes in central bundle could not be counted distinctly, but probably about 10.

Remarks.—With only fragmentary zoaria, the specific identification is deferred until better material is available.

Order Fenestrata Elias and Condra, 1957
Family Fenestellidae King, 1849
Genus ***Alternifenestella***Termier and Termier, 1971

Alternifenestella minor (Nikiforova, 1933)

Figure 3-2

Fenestella donaica (Lebedev) *a* Nikiforova, 1927, p. 249, pl. 12, fig. 5.

Fenestella donaica var. *minor* Nikiforova, 1933, p. 13, pl. 3, figs. 1-3; Nekhoroshev, 1948, p. 21, pl. 2, figs. 1a, b, pl. 10, fig. 4.

Fenestella minor Nikiforora. Shulga-Nesterenko, 1951, p. 89, pl. 1, figs. 3, 6, pl. 17, fig. 1, pl. 18, fig. 5; Trizna, 1958, p. 146, 147, pl. 42, fig. 1; Kodsi, 1967, p. 66, 67, pl. 2, figs. 1-4; Termier and Termier, 1971, p. 42, pl. 27, fig. 1.

Material.—DESC-95015 (Ya12a-2a), DESC-95025 (Ya12a-13a), ?DESC-95087 (Yb10a-3).

Horizon.—Uppermost part of *Triticites* zone at Yaurichambi-b and lower part of *Pseudoschwagerina* zone at Yaurichambi-a routes.

Description.—Zoarium consists of straight parallel branches connected by dissepiments at regular intervals. Branches bifurcate infrequently. Branches narrow, ranging from 0.154 to 0.192 mm and 17 to 20 branches in 10 mm horizontally. Fenestrules quadrate with rounded corners, wider than branches, width 0.282 to 0.488 mm, length 0.486 to 0.538 mm, 16 to 18 fenestrules per 10 mm length of branch. Width of dissepiment narrow, ranging from 0.064 to 0.090 mm. Zooecial tubes arranged in strongly alternating longitudinal series, typically rhomboidal in lower level of branch, trigonal in middle level, and strongly curved outward and becoming parallel to tangential direction of zoarium in upper level. Zooecial tubes near surface circular in tangential section, ranging from 0.080 to 0.090 mm in diameter, 16 to 18 zooecia per 5 mm longitudinally, consistent pattern of apertures in relation to dissepiments; 2 apertures per fenestrule. Nodes arranged regularly in one row on well-developed straight carina, 0.050 to 0.060 mm in diameter, and spaced at about the same interval as apertures, namely 17 to 18 per 5 mm length of branch. Stereom covering reverse side of branch consisting of inner semitransparent layer of colonial plexus and outer sclerenchyma of darker fine fibers without spicules.

Meshwork formula.—17-20/16-18//16-18/17-18* (*17-20 branches in 10 mm of zoarial width; 16-18 fenestrules in 10 mm zoarial length; 16-18 zooecia in 5 mm of branch length; 17-18 nodes in 5 mm of branch length).

Remarks.—The present form is closely similar to *Alternifenestella minor*, originally described as *Fenestella donaica* (Levedev) *a* by Nikiforova (1927) and later named *F. donaica* var. *minor* by Nikiforova (1933) from the middle Carboniferous of the Donetz basin. A slight difference in the meshwork formula between the original specimens from the Donetz basin and the present material is considered to be conspecific variation.

The narrower width of the branch in comparison to that of the fenestrule, the arrangement of zooecial tubes in strongly alternating longitudinal series and their strong curvature are distinctive characters of this species.

Alternifenestella **aff.** ***A. pajerensis*** (Chronic, 1949)

Figure 3-6

Fenestrellina pajerensis Chronic in Newell *et al.*, 1949, p. 123; Chronic in Newell *et al.*, 1953, p. 116, 117, pl. 22, figs. 1, 2.

Material.—DESC-95007 (Ya08b-1a), DESC-95009 (Ya08b-4b), DESC-95125 (Ma6, 1.5 m, up-4), DESC-95126 (Ma6, 1.5 m, up-5), DESC-95128 (Ma6, 1.5 m, up-7), DESC-95129 (Ma6, 1.5 m, up-8).

Horizon.—Middle part of *Triticites* zone at Matilde route, and lower part of *Pseudoschwagerina* zone at Yaurichambi-a route.

Description.—Zoarium consists of straight parallel branches connected by dissepiments at regular intervals. Branches probably bifurcated at very long intervals, but no bifurcating points observed on 13 mm branch length. Branch wider or almost as wide as that of fenestrule, ranging from 0.205 to 0.256 mm; 24 branches per 10 mm horizontally. Fenestrules quadrate with rounded corners; width ranging from 0.179 to 0.256 mm, length ranging from 0.320 to 0.448 mm; 18 to 20 fenestrules per 10 mm branch length. Dissepiments narrow, width ranging from 0.096 to 0.154 mm. Zooecial tubes arranged in strongly alternating longitudinal series; elongated trigonal at middle level of branch, curved outward and circular at upper level of branch, 0.064 to 0.090 mm in diameter. Distance between zooecial apertures from center to center ranges from 0.192 to 0.256 mm; 22 to 26 zooecia per 5 mm longitudinally, not consistently spaced in relation to dissepiments, usually 2.5 apertures per fenestrule. Well developed nodes arranged regularly in one row on straight carina. Nodes about 0.050 mm in outside diameter, and spaced at the same interval as apertures, namely 22 to 26 per 5 mm branch length. Stereom covering reverse side of branch consists of inner semitransparent layer of colonial plexus and outer sclerenchyma of darker fibers with minute spicules.

Meshwork formula.—24/18-20//22-26/22-26.

Remarks.—The present form may be identical with *Alternifenestella pajerensis* (Chronic), described from the Copacabana Group in Huanta, Peru because the meshwork formulae are very similar. However, detailed comparison is impossible because Chronic (in Newell et al., 1949, 1953) described only the silicified surface of the specimens.

Alternifenestella* (*Cervella*) *cervoides (Chronic, 1949)

Figure 3-1

Cervella cervoides Chronic in Newell *et al*., 1949, p. 124; Chronic in Newell *et al*., 1953, p. 118-119, pl. 23, figs. 3a-7.

Material.—DESC-95198 (Cu115-1), DESC-95199 (Cu115-3), DESC-95202 (Cu115-9), DESC-95227 (Yp65-24c).

Horizon.—Middle part of *Pseudoschwagerina* zone at Cuyavi and Yampupata routes.

Description.—Zoarium consists of straight parallel branches connected by dissepiments at regular intervals. Branches bifurcate at long intervals. Branch width ranges from 0.256 to 0.320 mm; 21 to 26 branches per 10 mm horizontally. Fenestrules quadrate with rounded corners, and with narrow width, usually less than half the width of a branch, ranging from 0.102 to 0.166 mm, length ranging from 0.192 to 0.358 mm; 24 to 30 fenestrules per 10 mm branch length. Dissepiments narrow, width ranging from 0.102 to 0.141 mm. Zooecial tubes arranged in alternately intersecting longitudinal series, usually trigonal at middle level of branch, curved outward and circular at upper level of branch, 0.090 to 0.115 mm in diameter. Distance between zooecial apertures from center to center ranges from 0.192 to 0.256 mm; 20 to 25 zooecia per 5 mm longitudinally per range, not consistently spaced in relation to dissepiment; less than 2 apertures per fenestrule. Well developed nodes arranged regularly in one row on straight carina, ranging from 0.050 to 0.077 mm in outside diameter; spaced at about the same interval as apertures; namely 20 to 25 nodes per 5 mm of branch length. Stereom covering reverse side of branch consists of inner semitransparent layer of colonial plexus and outer sclerenchyma of darker fibers with abundant, well-developed spicules.

Meshwork formula.—21-26/24-30//20-25/20-25.

Remarks.—The present form may belong to the Group XII *Fenestella spinulosa* Condra (Elias and Condra, 1957). It is nearest in principal measurements to *Cervella cervoides* which Chronic (in Newell *et al*., 1949) described as a member of his newly established genus *Cervella* from the Copacabana Group in Peru. Elias and Condra (1957) provisionally accepted *Cervella* as a polyphyletic subgenus of *Fenestella*.

My examination of many thin sections prepared from the Copacabana Group shows that the typical *Cervella* having a "superstructure" is not present any where. Although detailed comparison with the type which presents only surface features cannot be made, the present form may be identical with *Cervella cervoides*. It resembles *Alternifenestella aspera* (Chronic), but differs from the latter in the meshwork formula and the position of apertures in relation to dissepiment.

Alternifenestella* (*Cervella*) *aspera (Chronic, 1949)

Figure 3-3

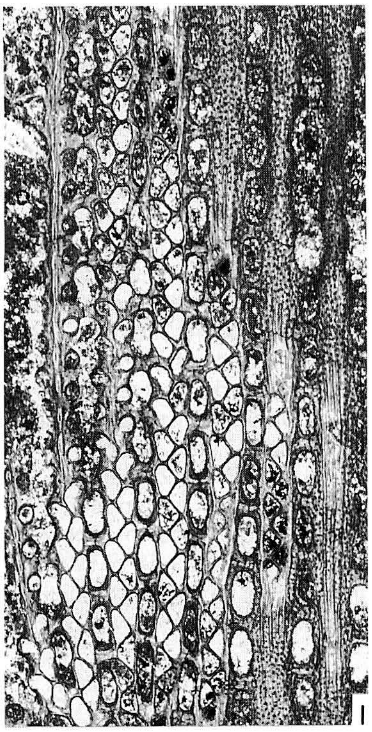
Cervella aspera Chronic in Newell *et al*., 1949, p. 125; Chronic in Newell *et al*., 1953, p. 119, pl. 23, figs. 1-2b.

Material.—DESC-95016 (Ya12a-3b), DESC-95024 (Ya12a-12), DESC-95026 (Ya12a-14). DESC-95027 (Ya12a-15), DESC-95030 (Ya12a-18), DESC-95195 (Cu114-35), DESC-95196 (Cu114-38), DESC-95197 (Cu114-40).

Horizon.—Lower part of *Pseudoschwagerina* zone at Yaurichambi-a and Cuyavi routes.

Description.—Form of zoarium is unknown but probably fan-shaped. Zoarium consists of straight parallel branches connected by dissepiments at regular intervals. Branches bifurcate at 10 mm intervals. Branch width ranges from 0.256 to 0.384 mm; 18 to 21 (26 branches in special case) per 10 mm horizontally. Fenestrules quadrate with rounded corners, width ranging from 0.128 to 0.230 mm and length ranging from 0.307 to 0.448 mm; 19 to 22 fenestrules per 10 mm of branch length. Width of dissepiment ranges from 0.090 to 0.128 mm. Zooecial tubes arranged in strongly alternating longitudinal series and usually triangular but occasionally pentagonal at lower to middle levels of branch, curved outward, and circular at upper level of branch; diameter ranges from 0.090 to 0.115 mm. Intervals between zooecial apertures from center to center range from 0.230 to 0.282 mm. Zooecial apertures 17 to 22 per 5 mm longitudinally, usually consistent in position in relation to dissepiments. Two apertures per fenestrule. Well-developed nodes arranged regularly in one row on straight carina. Nodes about 0.050 to 0.077 mm in outside diameter, and spaced

Figure 3. 1. *Alternifenestella* (*Cervella*) *cervoides* (Chronic), tangential section, ×20, DESC-95202 (Cu115-9). **2.** *Alternifenestella minor* (Nikiforova), tangential section, ×20, DESC-95025 (Ya12a-13a). **3.** *Alternifenestella* (*Cervella*) *aspera* (Chronic), tangential section, ×20, DESC-95030 (Ya12a-18). **4.** *Minilya binodata* (Condra), tangential section, ×20, DESC-95019 (Ya12a-6b). **5.** *Fabifenestella* sp. indet., tangential section, ×20, DESC-95224 (Yb65-2a). **6.** *Alternifenestella* aff. *A. pajerensis* (Chronic), tangential section, ×20, DESC-95007 (Ya08b-1a).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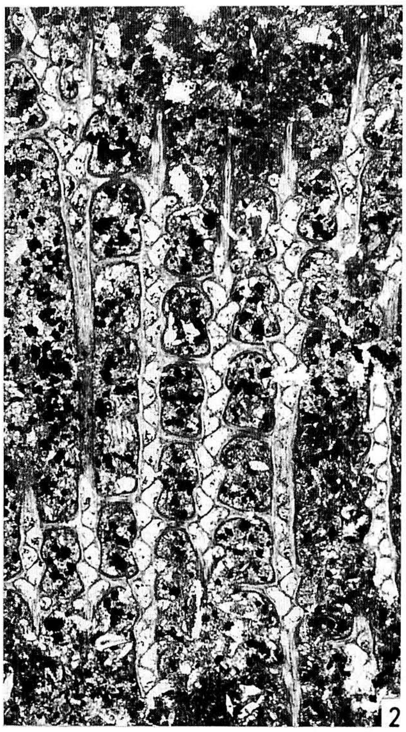
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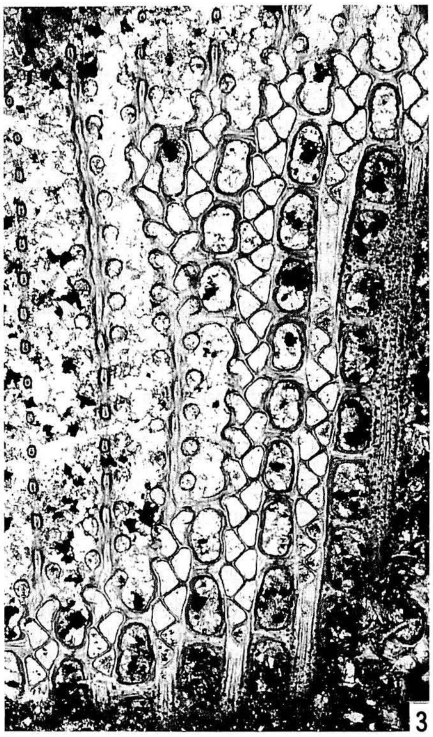
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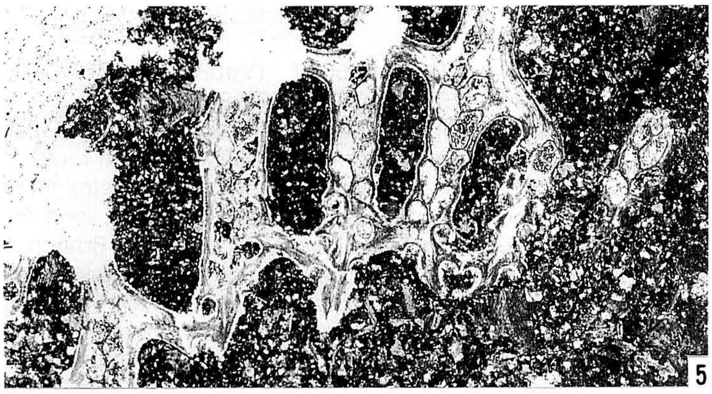
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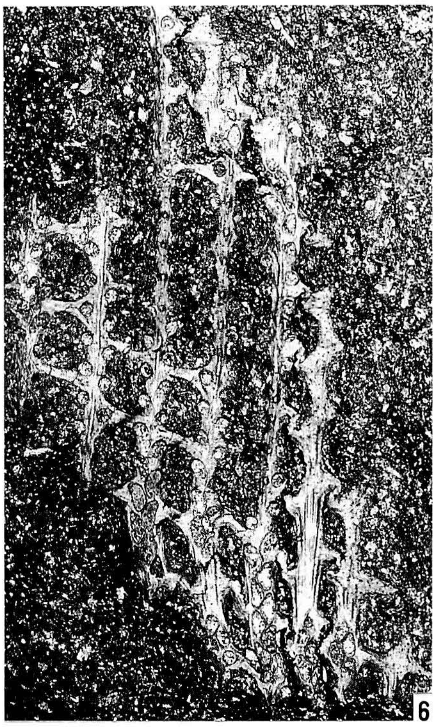
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at about the same interval as apertures, namely 18 to 21 per 5 mm of branch length. Stereom covers reverse side of branch, consists of inner semitransparent layer of colonial plexus and outer sclerenchyma of darker fibers with abundant, well developed spicules.

Meshwork formula.—18-21 (26)/19-22//17-22/18-21.

Remarks.—Although detailed comparison with the type, established on the surface features by Chronic (in Newell *et al*., 1953), cannot be made, the present form is similar to *Cervella aspera* in its principal measurements. The present species is characterized by prominent and regularly arranged nodes on a well developed carina.

Alternifenestella ? sp. indet.

Figure 4-3

Material.—DESC-95013 (Ya08b-8).

Horizon.—Upper part of *Triticites* zone at Yaurichambi-a route.

Description.—Zoarium consists of straight parallel branches connected regularly by dissepiments spaced at regularly long intervals. Branches bifurcate at long intervals. Branch width ranges from 0.256 to 0.320 mm and 14 to 18 branches per 10 mm horizontally. Fenestrules elongate, quadrate with rounded corners, width variable, ranging from 0.190 to 0.640 mm, length ranges from 0.960 to 1.120 mm; usually 8 fenestrules per 10 mm of branch length. Dissepiments narrow, width ranging from 0.154 to 0.166 mm. Zooecial tubes arranged in alternating longitudinal series and trigonal to pentagonal at middle level of branch, curved outward and oval at upper level of branch, 0.115 to 0.128 mm in shorter diameter near the surface. Distance between zooecial apertures from center to center ranges from 0.230 to 0.256 mm; 18 to 20 zooecia per 5 mm longitudinally per range, probably consistent spacing of apertures in relation to dissepiment, usually 5 apertures per fenestrule. Straight carina present but nodes obscure. Stereom covering reverse side of branch consists of inner semitransparent layer of colonial plexus and outer sclerenchyma of coarser fibers.

Meshwork formula.—14-18/8//18-20/?.

Remarks.—Only one poorly preserved specimen is available and this is insufficient for specific identification.

Genus **Minilya** Crockford, 1944

Minilya binodata (Condra, 1902)

Figure 3-4

Fenestella binodata Condra, 1902, p. 350-251, pl. 21, figs. 12, 13; Elias and Condra, 1957, p. 90.

Material.—DESC-95019 (Ya12a-6b).

Horizon.—Lower part of *Pseudoschwagerina* zone at Yaurichambi-a route.

Description.—Sample is a single tangential section showing features at all levels. Zoarium consists of straight parallel branches connected by dissepiments at regular intervals. Branches bifurcate at very long intervals. Branch almost as wide as or wider than that of fenestrule, ranging from 0.320 to 0.384 mm; 16 to 18 branches per 10 mm horizontally. Fenestrules elongate, quadrate with rounded corners; width ranges from 0.256 to 0.358 mm, length ranges from 0.704 to 0.896 mm; 10 to 11 fenestrules per 10 mm of branch length. Dissepiments range from 0.154 to 0.179 mm in width. Zooecial tubes arranged in very weakly alternating longitudinal series, kidney-shaped at middle level of branch, curved outward and circular at upper level, range from 0.090 to 0.102 mm in diameter. Intervals between zooecial apertures from center to center range from 0.230 to 0.320 mm. Zooecial apertures 14 to 16 per 5 mm length of one range, usually consistently spaced in relation to dissepiment, 3 apertures per fenestrule. Two rows of zigzag nodes prominent on well-developed broad carina. Total number of nodes range from 28 to 32 per 5 mm of branch length. Nodes range from 0.050 to 0.064 mm and are spaced at same interval as apertures, namely, one node to each zooecial aperture. Stereom covering reverse side of branch consisting of inner semitransparent layer of colonial plexus and outer sclerenchyma of darker fibers with very small granules.

Meshwork formula.—16-18/10-11//14-16/28-32.

Remarks.—The present form belongs to Group VII, *Fenestella* (*Minilya*) *binodata* Condra (Elias and Condra, 1957). In their systematic study of *Fenestella*, Condra and Elias established three varieties of *binodata*, namely, var. *wolfcampensis* from the Lower Wolfcampian, var. *leonardensis* from the Leonardian and var. *wordensis* from the Wordian of Texas. The present form is nearest in its measurements to the type *binodata* which Condra (1902) described from the Upper Virgilian Shawnee Group of Nebraska.

Genus **Fabifenestella** Morozova, 1974

Fabifenestella aff. ***F. huascatayana*** (Chronic, 1949)

Figure 4-2

Fenestrellina huascatayana Chronic in Newell *et al*., 1949, p. 120; Chronic in Newell *et al*., 1953, p. 114, 115, pl. 22, figs. 3a, b.

Material.—DESC-95007 (Ya08b-1), DESC-95010 (Ya08b-5), DESC-95022 (Ya12a-9).

Horizon.—Upper part of *Triticites* to lower part of *Pseudoschwagerina* zones at Yaurichambi-a route.

Description.—Zoarium consists of nearly straight parallel branches connected by dissepiments at long regular intervals. Branches bifurcate frequently. Branch width narrower than that of fenestrule, ranging from 0.288 to 0.320 mm; about 12 branches per 10 mm horizontally. Fenestrules elongate, quadrate with rounded corners; width ranges from 0.480 to 0.640 mm, length ranges from 1.440 to 1.760 mm, 5 to 6 fenestrules per 10 mm of branch length. Dissepiments narrow, ranging from 0.160 to 0.192 mm in width. Zooecial tubes form very limited alternating longitudinal series, elongated pentagon or trapezoid with

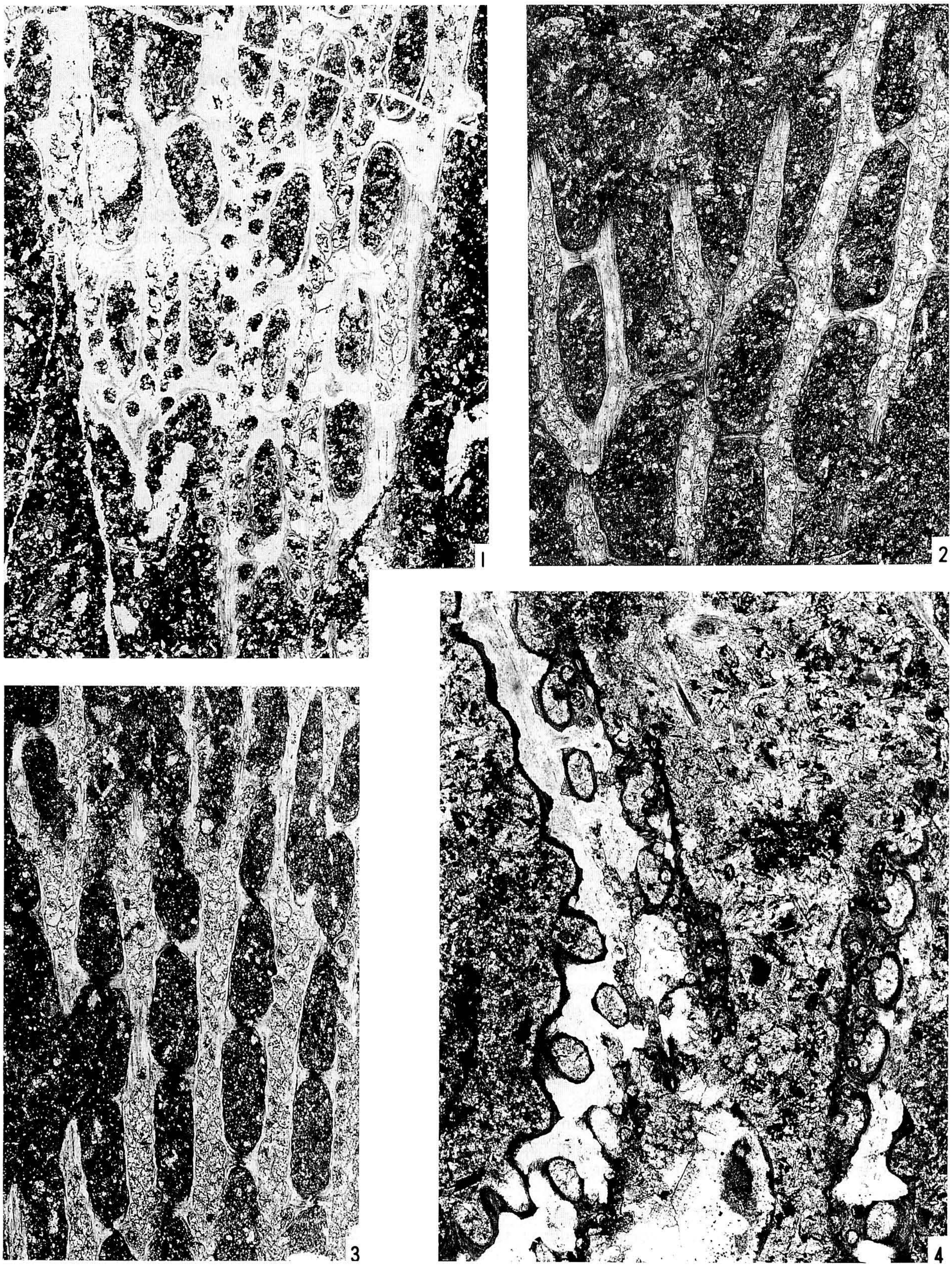

Figure 4. **1.** *Fabifenestella* sp. indet., tangential section, ×20, DESC-95215 (Yp65-11). **2.** *Fabifenestella* aff. *F. huascatayana* (Chronic), tangential section, ×20, DESC-95010 (Ya08b-5). **3.** *Alternifenestella* ? sp. indet., tangential section, ×20, DESC-95013 (Ya08b-8). **4.** *Polypora elliptica* Rogers, tangential section, ×20, DESC-95038 (Ya29b-6b).

well developed hemiseptum at lower level of branch, circular at upper level, range from 0.090 to 0.102 mm in diameter. Intervals between zooecial apertures from center to center range from 0.282 to 0.320 mm. Zooecial apertures 16 to 17 per 5 mm in a range; apertures usually consistently positioned in relation to dissepiment, 6 zooecia per fenestrule. Carina not prominent and nodes indistinct. Stereom covers reverse side of branch, consists of inner semitransparent layer of colonial plexus and outer sclerenchyma of darker fibers with very small granules.

Meshwork formula.—12/5-6//16-17/nothing.

Remarks.—The present form may be identical with *Fabifenestella huascatayana* (Chronic), described from the Copacabana Group in Pasaje-Picchu of Peru, because the meshwork formulae are very similar. However, detailed comparison is impossible because Chronic described only the silicified surface specimens. The present form resembles *Fabifenestella ajensis* (Trizna, 1950) described from the Lower Perminan of the Canadian Arctic Archipelago by Morozova and Kruchinina (1986) in general features, but it can be distinguished from the latter species by the larger number of zooecial tubes per 5 mm of branch length (16-17 instead of 12-13).

Fabifenestella sp. indet.

Figures 3-5; 4-1

Material.—DESC-95015 (Ya12a-2b), DESC-95215 (Yp65-11), DESC-95224 (Yp65-21a).

Horizon.—Upper part of *Triticites* zone at Yaurichambi-a route, and middle part of *Pseudoschwagerina* zone at Yaurichambi-a and Yampupata routes.

Description.—Zoarium consists of nearly straight branches connected by dissepiments at regular intervals. Branches bifurcate frequently, at about every 3 fenestrules. Width of branch usually narrower than that of fenestrule, ranging from 0.320 to 0.480 mm; 12 to 14 branches per 10 mm horizontally. Fenestrules quadrate with rounded corners, width ranging from 0.320 to 0.640 mm, length 0.800 to 1.280 mm; 7 to 9 fenestrules per 10 mm of branch length. Dissepiments narrow, range from 0.192 to 0.250 mm in width. Zooecial tubes in limited alternating longitudinal series, usually trapezoid or deformed pentagonal at lower to middle levels of branch, and circular at upper level, range from 0.115 to 0.128 mm in diameter. Zooecial apertures 16 to 18 per 5 mm in a range, not consistently positioned in relation to dissepiments but usually 4 to 5 zooecia per fenestrule. Nodes present, but not distinct in arrangement. Stereom covering reverse side of branch consists of inner semitransparent layer of colonial plexus and outer darker fibers with small granules.

Meshwork formula.—12-14/7-9//16-18/?.

Remarks.—The present form has some similarity to *Fabifenestella huascatayana* in the meshwork formula, but is distinguished by the number of zooecia per fenestrule, namely 4 to 5 zooecia in the present form and 6 in the latter species. The specific identification is postponed until more specimens are available.

Genus ***Polypora*** McCoy, 1844

Polypora elliptica Rogers, 1900

Figures 4-4; 5-1

Polypora elliptica Rogers, 1900, p. 7, 8, pl. 4, fig. 2; Moore, 1929, p. 23, 24, pl. 3, figs. 7, 8, 20.

Polypora elliptica (s.s.) Rogers. Elias, 1937, p. 327, 328, fig. 3m.

Material.—DESC-95038 (Ya29b-6), DESC-95064 (Ya38a(up)-1c), DESC-95099 (Yc21a-7).

Horizon.—Lower to middle part of *Eoparafusulina* zone at Yaurichambi-a and -b routes.

Description.—Zoarium consists of straight, parallel branches connected by dissepiments at regular intervals. Branches bifurcate infrequently. Branch width about twice that of fenestrule, ranging from 0.320 to 0.576 mm; usually 14 to 16 branches per 10 mm horizontally. Fenestrules oval in outline; width ranges from 0.192 to 0.320 mm; length from 0.352 to 0.480 mm; usually 12 to 14 per 10 mm of branch length. Dissepiments broad, width ranges from 0.256 to 0.480 mm. Zooecial tubes usually 3 rows but occasionally 4 rows across a branch, and before bifurcation 5 rows; just after bifurcation 2 rows; elongate quadrate or elongate hexagonal zooecia at middle and lower levels of branch because of slightly alternating intercalated zooecial tubes in longitudinal series. Zooecial tubes circular in tangential section near surface, ranging from 0.102 to 0.128 mm in diameter. Number of zooecial apertures ranges from 19 to 21 per 5 mm length of one range, usually 3 apertures per fenestrule. Interspaces between zooecial apertures from center to center range from 0.230 to 0.320 mm longitudinally. Stereom covers reverse side of branch, consists of semitransparent layer of colonial plexus with some capillary canals and outer sclerenchyma of darker fibers with well developed fine granules.

Meshwork formula.—14-16/12-14//18-21/3(2-4)*(*14-16 branches in 10 mm of zoarial width; 12-14 fenestrules in 10 mm of zoarial length; 18-21 zooecia in 5 mm of branch length; 3 (2-4) number of rows of zooecia).

Remarks.—Elias (1937) discussed the evolutionary changes in the *Polypora elliptica* Group, which include a range as homogeneous stretching of the zoarium in both longitudinal and transverse directions. The present form is closely similar to *Polypora elliptica* (s.s.) in its principal measurements and features. Rogers (1900) described *P. elliptica* from the Kereford limestone of the Oread Formation, which is now dated as the Middle Virgilian.

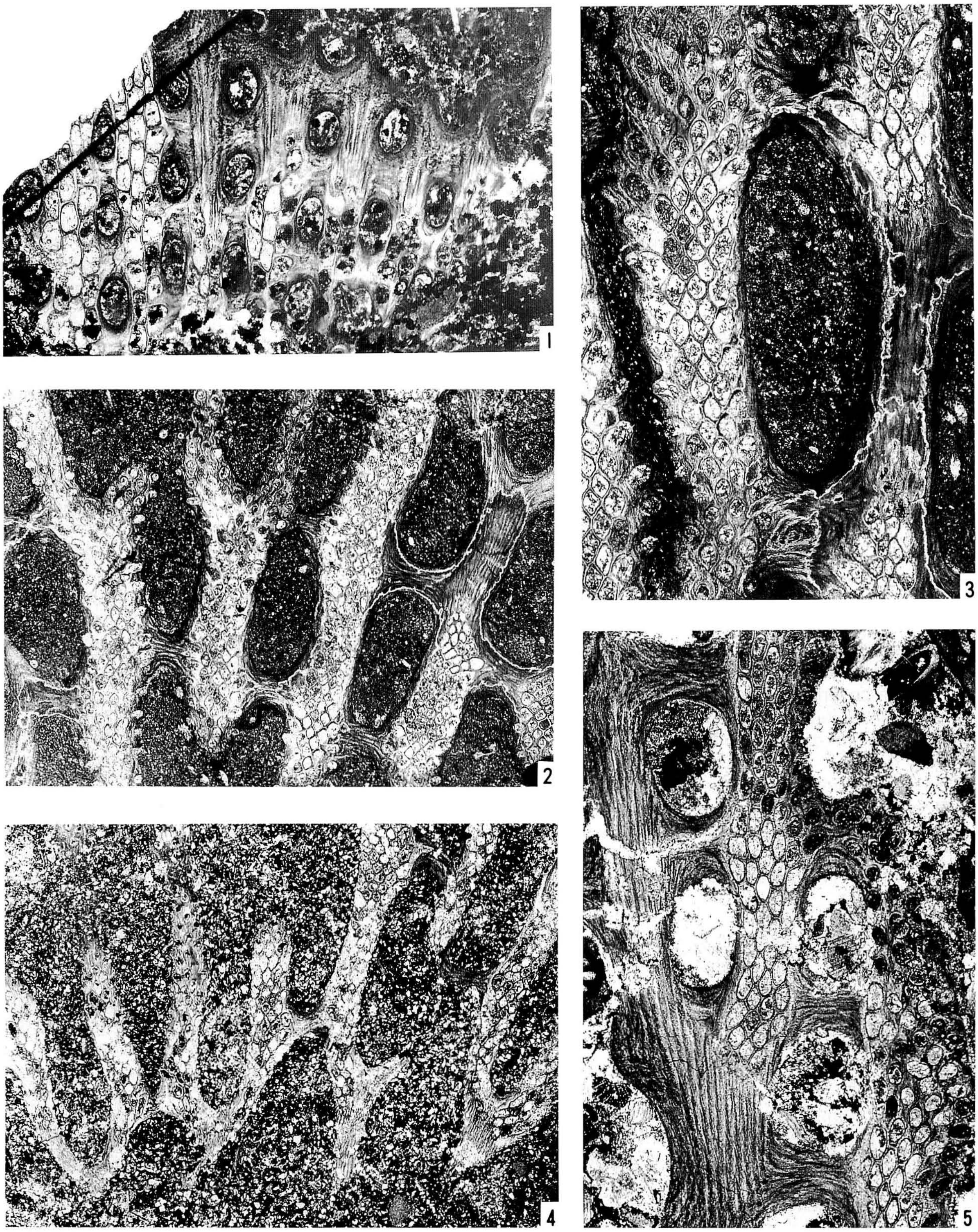

Figure 5. **1.** *Polypora elliptica* Rogers, tangential section, ×20, DESC-95099 (Yc21a-7). **2-4.** *Polypora* cf. *P. megastoma* (Koninck), 2, 4 : tangential sections, ×10, DESC-95011 (Ya08b-6) and DESC-95209 (Yp65-3), respectively. 3 : enlarged part of 2, ×20. **5.** *Polypora cyclopora* Eichwald, tangential section, ×20, DESC-95043 (Ya33b-4b).

Polypora cyclopora Eichwald, 1860

Figures 5-5; 6-1

Polypora cyclopora Eichwald, 1860, p. 375, pl. 30, fig. 1; Stuckenberg, 1895, p. 156, pl. 12, fig. 4; Nikiforova, 1938, p. 140-142, 250, pl. 33, figs. 1-6, pl. 34, figs. 1, 2; Shulga-Nesterenko, 1941, p. 161, 162, pl. 44, figs. 1-3, text-figs. 125, 126.

Material.—DESC-95043 (Ya33b-4b), DESC-95112 (An38-2), DESC-95187 (Cu114-14), DESC-95190 (Cu114-26), DESC-95192 (Cu114-30).

Horizon.—Upper (?) part of *Pseudoschwagerina* zone at Cuyavi route, and lower to middle part of *Eoparafusulina* zone at Yaurichambi-a and Ancoraimes routes.

Description.—Zoarium consists of straight, parallel branches connected by dissepiments at regular intervals. Branches bifurcate infrequently. Branch width wider than that of fenestrule, ranging from 0.640 to 0.960 mm, 6 to 7 branches per 10 mm horizontally. Fenestrules oval in outline, width ranging from 0.576 to 0.800 mm, length from 0.960 to 1.440 mm; usually 5 to 6 per 10 mm of branch length. Dissepiments broad, width 0.480 to 0.800 mm. Zooecial tubes usually in 6 to 7 rows on each branch, but before bifurcation increasing to 7 to 9 rows, after bifurcation 5 rows; 16 to 18 per 5 mm length of one range, usually 6 to 7 apertures per fenestrule. Zooecial tubes arranged in strongly alternating longitudinal series and usually rhomboidal or hexagonal at middle level of branch. Diameter of zooecial tube near surface ranges from 0.102 to 0.128 mm. Distance between zooecial apertures from center to center ranges from 0.230 to 0.256 mm longitudinally. Stereom covering reverse side of branch consists of inner semitransparent layer of colonial plexus and outer sclerenchyma of darker fibers with fine granules.

Meshwork formula.—6-7/5-6//16-18/6-7.

Remarks.—The present form is similar to *Polypora cyclopora* described from European Russia in the meshwork formula and internal structures. However, the number of fenestrules in 10 mm length are slightly different, namely, 5 to 6 in the present form and usually 4 in the Russian form.

Polypora aff. ***P. inimica*** Chronic, 1949

Figures 6-3, 4

Polypora inimica Chronic in Newell *et al.*, 1949, p. 127; Chronic in Newell *et al.*, 1953, p. 121, pl. 26, figs. 1a, b.

Material.—DESC-95168 (Cu113-9b), DESC-95172 (Cu113-13), DESC-95191 (Cu114-28), DESC-95196 (Cu114-38), DESC-95211 (Yp65-7), DESC-95228 (Yp67-2).

Horizon.—Middle to upper (?) part of *Eoparafusulina* zone at Cuyavi and Yampupata routes.

Description.—Zoarium consists of straight, parallel branches connected by dissepiments at regular intervals. Branches bifurcate infrequently. Branch width wider than that of fenestrule, ranging from 0.480 to 0.800 mm; usually 8 to 10 branches per 10 mm horizontally. Fenestrule oval in outline; width ranging from 0.384 to 0.640 mm; length from 0.800 to 1.120 mm, usually 7 to 8 per 10 mm of branch length. Dissepiments of moderate width in comparison to branches, ranging from 0.384 to 0.416 mm. Zooecial tubes arranged usually in 5 rows on each branch, but before bifurcation 6 rows, after bifurcation 3 rows; rhomboidal at middle level of branch because of strongly alternating, intercalated zooecial tubes in longitudinal series. Zooecial tubes circular in tangential section near surface, ranging from 0.115 to 0.128 mm in diameter. Number of zooecial apertures ranges from 17 to 18 per 5 mm length of one range, usually 5 apertures per fenestrule. Interspaces between zooecial apertures from center to center range from 0.230 to 0.256 mm longitudinally. Nodes less than 0.050 mm in outside diameter, at each intersection of zooecial apertures. Stereom covers reverse side of branch, consists of semitransparent layer of colonial plexus with many capillary canals and outer sclerenchyma of dark coarser fibers with fine granules.

Meshwork formula.—8-10/7-8//17-18/5.

Remarks.—The present form may be identical with *Polypora inimica* Chronic, described from the Copacabana Group in Peru in terms of the meshwork formula, but a detailed comparison cannot be made because the type specimens were described only for their surface features. The present form resembles *Polypora cyclopora*, but differs in the meshwork formula and by the presence of one node beside each zooecial tube. In the specimens from Yp65-7 and Yp67-2 the nodes are obscure but the specimens are similar in the meshwork formula and other characteristics to the Cuyavi specimens.

Polypora cf. ***P. megastoma*** (Koninck, 1863)

Figures 5-2—4

Fenestella megastoma Koninck, 1863, p. 5, pl. 2, fig. 3.

Polypora megastoma (Koninck). Waagen and Pichl, 1885, p. 785, 786, pl. 88, figs. 3, 5-7, pl. 89, fig. 3; Stuckenberg, 1895, p. 238, pl. 23, fig. 7; Fritz, 1932, p. 101; Nikiforova, 1938, p. 146, pl. 33, fig. 10; Crockford, 1957, p. 61, pl. 16, figs. 2, 3.

Material.—DESC-95007 (Ya08b-1c), DESC-95008 (Ya08b-3), DESC-95009 (Ya08b-4), DESC-95011 (Ya08b-6), DESC-95012 (Ya08b-7), DESC-95019 (Ya12a-16), DESC-95201 (Cu115-6), DESC-95209 (Yp65-3), DESC-95212 (Yp65-8), DESC-95219 (Yp65-16a, b), DESC-95226 (Yp65-23).

Horizon.—Upper part of *Triticites* zone to lower part of *Pseudoschwagerina* zone at Yaurichambi-a route, and middle to upper (?) part of *Pseudoschwagerina* zone at Cuyavi and Yampupata routes.

Description.—zoarium consists of straight, parallel, robust branches connected by dissepiments at regular intervals. Branches bifurcate frequently. Branch width ranges from 0.800 to 1.280 mm; 4 to 8 branches per 10 mm horizontally. Fenestrules elongate, oval to elliptical in outline; width ranges from 0.576 to 1.280 mm; length ranges from 2.240 to 3.840 mm; 2 to 4 per 10 mm length of branch. Width of dissepiments varies from 0.416 to

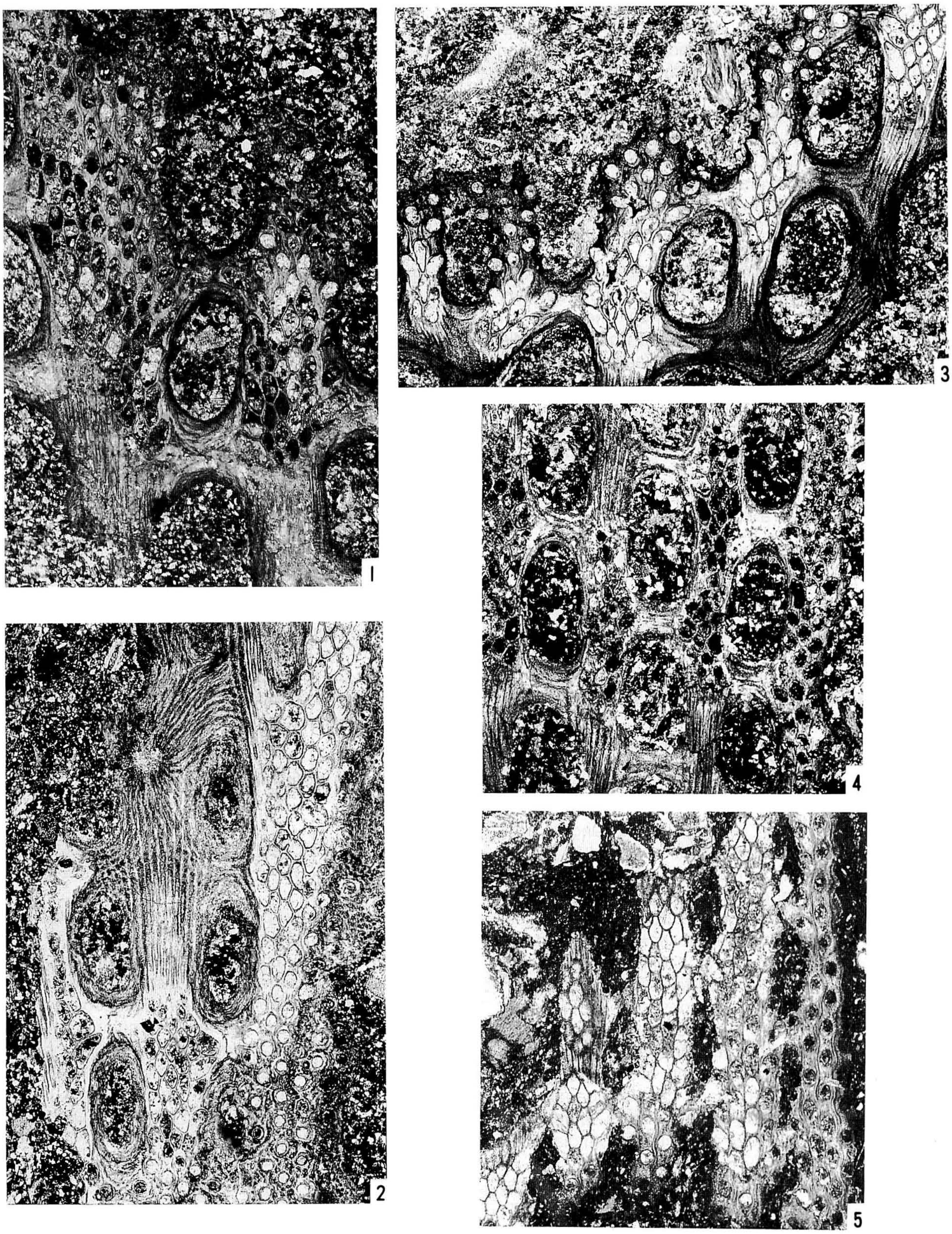

Figure 6. **1.** *Polypora cyclopora* Eichwald, tangential section, ×20, DESC-95187 (Cu114-14). **2.** *Polypora* sp. indet. A, tangential section, ×20, DESC-95101 (Yc21a-9). **3, 4.** *Polypora* aff. *P. inimica* Chronic, tangential sections, ×20, DESC-95168 (Cu113-9b) and DESC-95211 (Yp65-7). **5.** *Polypora* sp. indet. B, tangential section, ×20, DESC-95161 (Cu98-1).

0.900 mm. Zooecial tubes arranged in strongly alternating longitudinal series usually rhomboidal at middle level of branch, 6 to 7 rows on each branch, before bifurcation 8 rows, after bifurcation 5 rows ; 13 to 15 per 5 mm length of one range, usually 10 apertures per fenestrule. Diameter of zooecial tube near surface ranges from 0.115 to 0.141 mm. Distance between zooecial apertures from center to center ranges from 0.320 to 0.384 mm longitudinally. Thick stereom covers reverse side but on obverse side relatively thin, consists of inner semitransparent layer of colonial plexus and outer sclerenchyma of dark coarser fibers with fine granules.

Meshwork formula.—4-8/2-3//13-15/6-7.

Remarks.—The present form, characterized by very large meshwork, falls undoubtedly under the group of *Polypora megastoma* (Koninck) described from the Middle *Productus* limestone of Pakistan by Waagen and Pichl (1885) and *Polypora sugiyamae* Sakagami (1961) described from the *Parafusulina* zone in Japan. Although there are slight differences between these Tethyan species, the present form is conspecific with *Polypora megastoma*, which has a wide distribution.

Polypora sp. indet. A

Figure 6-2

Material.—DESC-95101 (Yc21a-9).

Horizon.—Lower part of *Eoparafusulina* zone (*Aviculopinna* horizon) at Yaurichambi-c route.

Description.—This single zoarium consists of straight, parallel branches connected by robust dissepiments at regular intervals. Bifurcation of branches not observed in ca. 15 mm length. Branch width about twice that of fenestrule, ranging from 0.800 to 0.960 mm ; about 8 branches per 10 mm horizontally. Fenestrules oval in outline ; width ranging from 0.320 to 0.480 mm, length from 0.800 to 0.960 mm ; usually 6 per 10 mm of branch length. Dissepiments very strong ; width ranges from 0.580 to 0.960 mm. Zooecial tubes arranged in 5 to 6 rows on each branch, and rhomboidal at middle level of branch because of arrangement of very strongly alternating intercalated zooecial tubes in longitudinal series. Zooecial tubes circular in tangential section near surface, ranging from 0.102 to 0.115 mm in diameter. Number of zooecial apertures ranges from 18 to 20 per 5 mm length of range, usually 6 apertures per fenestrule. Interspaces between zooecial apertures from center to center range from 0.243 to 0.282 mm longitudinally. Thick stereom covers reverse side of branch, consists of semitransparent layer of colonial plexus with many capillary canals and outer sclerenchyma of dark coarser fibers with many prominent spicules about 0.025 mm in maximum diameter.

Meshwork formula.—8/6//18-20/5-6.

Remarks.—The present form is characterized by robust dissepiments and many large spicules in the outer sclerenchyma. However, comparison with previously described species is not possible until better preserved specimens are found.

Polypora sp. indet. B

Figure 6-5

Material.—DESC-95161 (Cu98-1).

Horizon.—Middle part of *Pseudoschwagerina* zone at Cuyavi route.

Description.—This single zoarium consists of straight, parallel branches connected by dissepiments at regular intervals. Bifurcation of branches not observed in this specimen. Branch width ranges from 0.576 to 0.640 mm ; 12 to 13 branches per 10 mm horizontally. Fenestrules elongate, elliptical in outline, width very narrow, from 0.160 to 0.256 mm, length from 0.640 to 0.800 mm, usually 9 to 10 per 10 mm length of branch. Dissepiments very short but wide for the branch, ranging from 0.320 to 0.384 mm. Zooecial tubes arranged in 4 rows on each branch, more or less elongate hexagons at middle level of branch because zooecial tubes in longitudinal series are not so strongly alternatingly intercalated. Each row of zooecial tubes divided distinctly by meandering longitudinal striations. Zooecia circular in tangential section near surface, ranging from 0.102 to 0.115 mm in length, usually 4 apertures per fenestrule. Interspaces between zooecial apertures from center to center range from 0.281 to 0.320 mm longitudinally. Stereom covers reverse side of branch, consists of semitransparent layer of colonial plexus with several capillary canals and outer sclerenchyma of dark coarser fibers with fine granules.

Meshwork formula.—12-13/9-10//18-20/4.

Remarks.—The characteristics of the present form are : each row of zooecial tubes is distinguished by meandering striations ; very short dissepiments ; and accordingly very narrow fenestrule.

Polypora sp. indet. C

Figures 7-1, 2

Materials.—DESC-95142 (Ma32-1c), DESC-95144 (Ma32-3b), DESC-95145 (Ma32-4c), DESC-95146 (Ma32-5c).

Horizon.—Lower part of *Eoparafusulina* zone (*Aviculopinna* horizon) at Matilde route.

Description.—Zoarium consists of straight, parallel, robust branches connected by dissepiments at regular intervals. Bifurcation of branches not observed. Branch width wider than that of fenestrule, ranging from 0.960 to 1.120 mm ; usually 6 to 7 branches per 10 mm horizontally. Fenestrules nearly circular to oval in outline, width ranging from 0.640 to 0.960 mm, length from 1.120 to 1.280 mm, usually 6 per 10 mm of branch length. Dissepiments robust for the branch, ranging from 0.576 to 0.704 mm in width. Zooecial tubes arranged usually in 7 rows on each branch, more or less deformed rhomboids at middle level of branch because of arrangement of strongly alternating intercalated zooecial tubes in longitudinal series. Zooecial tubes circular in tangential section near surface, ranging from 0.115 to 0.128 mm in diameter, 20 to 22 per 5 mm length of range ; usually 6 to 7 per fenestrule. Inter-

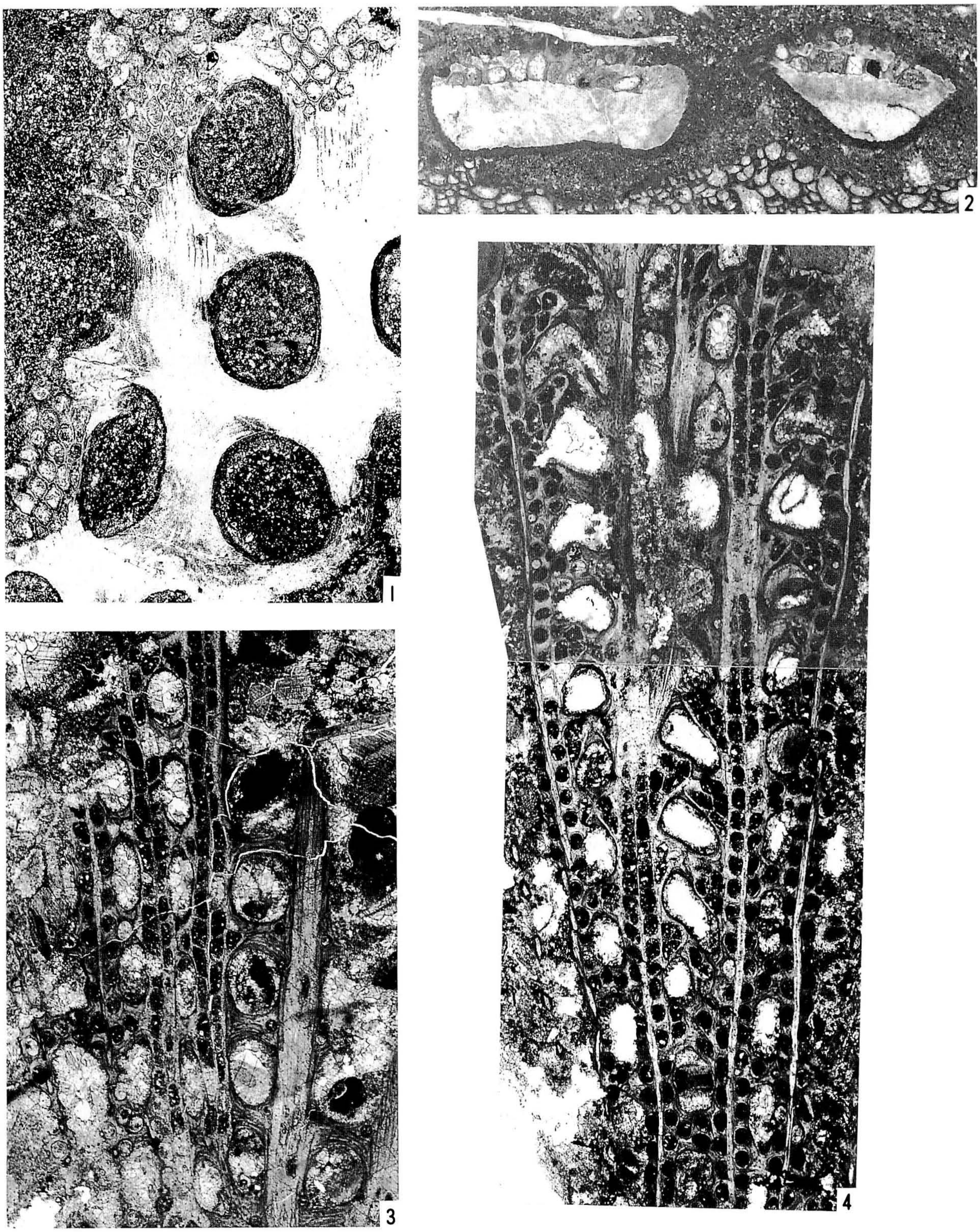

Figure 7. **1, 2.** *Polypora* sp. indet. C, tangential and transverse sections, ×20, DESC-95145 (Ma32-4c) and DESC-95146 (Ma32-5c), respectively. **3, 4.** *Septopora lineata* Nikiforova, tangential sections, ×20, DESC-95044 (Ya33b-6) and DESC-95039 (Ya32b-1), respectively.

spaces between zooecial apertures from center to center range from 0.230 to 0.282 mm longitudinally. Stereom covers reverse side of branch, consists of semitransparent layer of colonial plexus with many fine capillary canals and outer sclerenchyma of rather thin, dark fibers with fine granules.

Meshwork formula.—6-7/6//20-22/7.

Remarks.—The present form can be distinguished by the nearly circular to oval form of the fenestrules. *Polypora macrops* described from the Permian of Timor Island by Bassler (1929) has also rounded fenestrules, but it can be easily distinguished from the present form by the larger number of branches and fenestrules in 10 mm. The number of zooecial rows across the branch is quite different; 7 in the present form and 4 in *P. macrops.*

Family Septoporidae Morozova, 1962

Genus **Septopora** Prout, 1859

Septopora andeana sp. nov.

Figures 8-1, 2

Material.—Holotype: DESC-95035 (Ya20a-4); Paratypes: DESC-95036 (Ya20a-5), DESC-95037 (Ya21b-2).

Horizon.—Upper part of *Pseudoschwagerina* zone at Yaurichambi-a route.

Description.—Zoarium probably fan-shaped, consists of straight, nearly parallel branches connected by dissepiments at regular intervals. Branches bifurcated at long intervals. Branch width usually ranges from 0.512 to 0.640 mm, occasionally 0.800 mm; 6 to 8 branches per 10 mm horizontally. Fenestrules usually irregular quadrangles with rounded corners or somewhat crescentic, as wide as or wider than branches, width ranging from 0.480 to 0.960 mm; 1.280 mm occasionally, length ranging from 0.640 to 0.800 mm; usually 8 to 9 fenestrules per 10 mm length of branch. Dissepiments have zooecial tubes, narrower than those of branches, width ranging from 0.480 to 0.640 mm. Zooecial tubes arranged in 2 rows on each main branch, 20 to 22 per 5 mm length of range, parallelogram or elongated quadrate in outline at lower to middle levels of branch because of no intercalated zooecial tubes in longitudinal series; 5 zooecia per fenestrule. Usually 10 to 14 zooecial tubes in 2 to 3 rows on each dissepiment. Diameter of zooecial tubes near surface ranges from 0.128 to 0.154 mm. Distance between zooecial apertures from center to center 0.230 to 0.256 mm longitudinally. Nodes in one row on straight carina and distance between nodes ranges from 0.282 to 0.384 mm; number of nodes per 5 mm unknown. Stereom covers reverse side of branch and is thin; detailed structures obscure because of secondary mineralization. Outer sclerenchyma of obverse side consists of coarse fibers with fine granules.

Meshwork formula.—8/8-9//20-22.

Remarks.—This new species seems to be similar to *Septopora subquadrans*, described by Ulrich (1890) from the upper limestones of the Chester Group in Kentucky and Illinois, U.S.A. However, the new species can be distinguished from the latter species in the meshwork formula (namely 10/10.5//21 in *S. subquadrans*).

Septopora lineata Nikiforova, 1933

Figures 7-3, 4; 8-3

Septopora subquadrans var. *lineata* Nikiforova, 1933, p. 28, 29, pl. 6, fig. 7, text-figs. 9, 10.

Septopora diamorpha Loo, 1958, p. 297, 303, pl. 2, fig. 4.

Material.—DESC-95039 (Ya32b-1), DESC-95040 (Ya32b-5), DESC-95044 (Ya33b-6b), DESC-95048 (Ya34a-8), DESC-95100 (Yc21a-8).

Horizon.—Lower part of *Eoparafusulina* zone (*Aviculopinna* horizon) at Yaurichambi-a and -c routes.

Description.—Zoarium fan-shaped, consists of straight, parallel branches connected by dissepiments having zooecia at regular intervals. Branches bifurcate at long intervals. Branch width ranges from 0.384 to 0.544 mm; 12 to 16 branches per 10 mm horizontally. Fenestrules variable in form and size, circular where small in size and irregularly polygonal with rounded or somewhat crescentic corners when larger; width varying from 0.192 to 0.800 mm, length from 0.384 to 0.576 mm; 11 to 14 fenestrules per 10 mm of branch length. Dissepiments have zooecial tubes, are about as wide as the branches, from 0.384 to 0.448 mm. Zooecial tubes arranged in 2 rows on each main branch, 21 to 25 per 5 mm length of one range, parallelogram or elongated quadrate in shape at lower to middle levels of branch because of no intercalated zooecial tubes in longitudinal series; usually 3 to 4 zooecia per fenestrule. Usually less than 10 zooecial tubes in 2 rows on each dissepiment. Diameter of zooecial tubes near surface ranges from 0.115 to 0.128 mm and distance between zooecial apertures from center to center 0.205 to 0.230 mm longitudinally. Nodes in one row on well developed straight carina; distance between nodes ranges from 0.384 to 0.448 mm; 11 to 13 (but 7-8 ? in Yc21a-8) per 5 mm of branch length. Stereom covers reverse side of branch, consists of inner semitransparent layer of colonial plexus with some capillary canals and outer sclerenchyma of darker fibers with coarse granules.

Meshwork formula.—12-16/11-14//21-25.

Remarks.—The present form is similar to *Septopora lineata* in its principal measurements and characters. *S. lineata* was described originally from the Djulfa region of Armenia by Nikiforova (1933) from the Gnishik horizon (Lower Guadalupian), and was also described from the Lower Permian Chihsia limestone in South China as *S. diamorpha* Loo (1958) (Morozova in Ruzhentsev and Sarycheva, 1965).

Septopora incaica (Chronic, 1949)

Figures 8-4, 5

Silvaseptopora incaica Chronic in Newell *et al.*, 1949, p. 132; Chronic in Newell *et al.*, 1953, p. 125-127, pl. 26, figs. 2-8b.

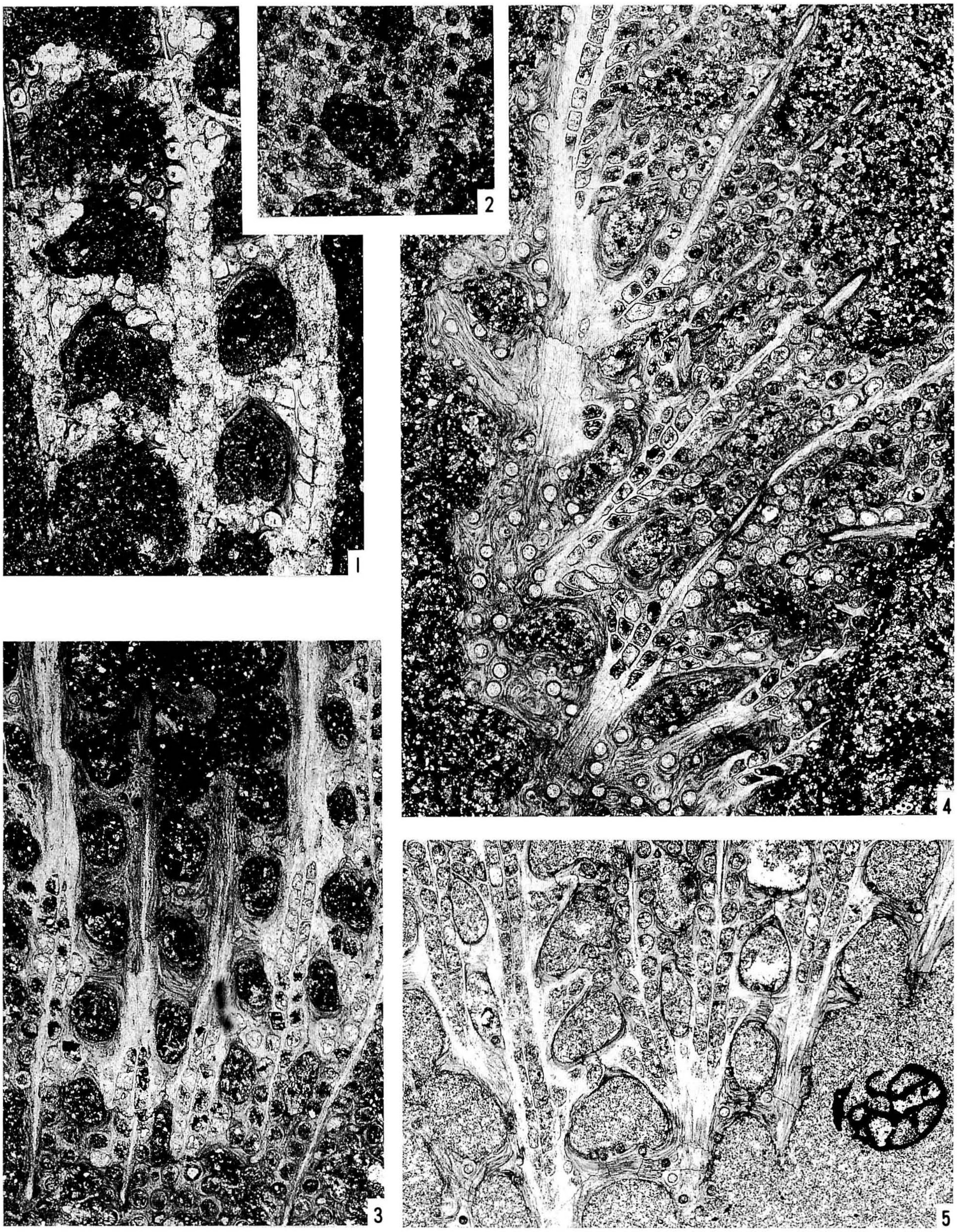

Figure 8. **1, 2.** *Septopora andeana* sp. nov., tangential sections, ×20, holotype (DESC-95035 (Ya20a-4)) and paratype (DESC-95037 (Ya21b-2)), respectively. **3.** *Septopora lineata* Nikiforova, tangential section, ×20, DESC-95100 (Yc21a-8c). **4, 5.** *Septopora incaica* (Chronic), tangential sections, ×20, DESC-95041 (Ya34-1) and DESC-95153 (Ma37 (20 cm below)-3b), respectively.

Material.—DESC-95046 (Ya34-1), DESC-95153 (Ma37 (20 cm, below)-3b).

Horizon.—Lower part of *Eoparafusulina* zone at Yaurichambi-a and Matilde routes.

Description.—Zoarium widespread, fan-shaped, consists of nearly straight branches connected by dissepiments at regular intervals. Pinnate branches with primary and secondary patterns. Branch width varies from 0.576 to 0.800 mm; 8 to 10 branches per 10 mm horizontally. Fenestrules of irregular shape such as polygons with rounded corners, crescentic corners in some cases, narrower than branches, width ranging from 0.320 to 0.480 mm, length from 0.576 to 0.800 mm; usually 7 to 9 fenestrules per 10 mm of branch length. Dissepiments have usually less than 10 but occasionally more than 10 zooecial apertures in 3 intersecting rows, ranging from 0.576 to 0.800 mm in width. Zooecial tubes arranged in 2 rows, occasionally 3 on each branch, 21 to 23 per 5 mm length of range, elongate quadrate or parallelogram at lower to middle level of branch, because of no intercalated zooecial tubes in longitudinal series; 5 to 6 zooecia per fenestrule. Diameter of zooecial tubes near surface ranges from 0.115 to 0.128 mm. Distance between zooecial apertures from center to center ranges from 0.230 to 0.256 mm longitudinally. Nodes in one row on prominent straight carina; distance between nodes ranges from 0.576 to 0.768 mm; 7 to 8 nodes per 5 mm length. Stereom covers reverse side of branch, consists of inner semitransparent layer of colonial plexus with some capillary canals and outer sclerenchyma of darker, coarse fibers with fine granules.

Meshwork formula.—8-10/7-9//21-23.

Remarks.—Chronic (in Newell, 1949, 1953) erected the genus *Silvaseptopora* having zoarial characters of *Septopora* but with the obverse surface heavily covered with erect spines of various sizes. Although the prominent spines are not observed in the specimens at hand, the present form can be identified with the type species of the genus, namely *Silvaseptopora incaica*, described from the Copacabana Group in Peru, in principal measurements and other characters, especially the zooecial arrangement in dissepiments. *Silvaseptopora* is now considered a junior synonym of *Septopora* because the generic characteristics described by Chronic do not seem to have taxonomic significance. The present species is not unlike *Septopora robusta*, described from the Upper Coal Measures in Illinois by Ulrich (1890), in morphological appearance, but the principal measurements of meshwork are different, the meshwork formula of the Illinois specimens being 5-8/7-8//22-23.

Acknowledgments

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999 Marsh foraminiferal and vegetation distributions in Nemuro Bay wetland areas, eastern Hokkaido

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Abstract. Although much work has been done on brackish water foraminifera, this is the first report of modern marsh foraminifera from Japan. Two transects were sampled in marshes of eastern Hokkaido for salt marsh foraminifera. Although these marshes were tidal, salinities were very low as evidenced by the freshwater plants that dominated the transects. Foraminifera present were low in diversity but extremely high in abundance-some of the highest ever recorded for a salt marsh. *Miliammina fusca* dominated lower areas together with *Trochammina macrescens* f. *macrescens* which dominated at all levels in both trasects. In the upper elevations of both transects, *Haplophragmoides manilaensis* became prominent and thecamoebians occupied the upland regions. Vertical zonation was generally poorly developed in both the foraminiferal and vegetation distributions which is typical of very brackish regions with low tidal ranges. Many typical brackish foraminiferal species observed in the Atlantic marshes are either rare or completely absent here.

Key words : Marsh foraminifera, eastern Hokkaido, vegetation zones, foraminiferal zones

Introduction

Although a sizeable amount of information on salt marsh foraminifera is now available from a wide variety of localities, to our knowledge, no one has previously examined modern salt marsh foraminifera from Japan. Many studies have been done on all shallow water environments in Japan by many Japanese workers starting in the last century but in most cases there was no marsh associated with the adjacent estuaries. Only in the eastern tip of Hokkaido in rather remote areas, are there still marshes left in their original state.

Because marsh deposits are now being used extensively to study rapid coastline changes associated with major earthquakes (Atwater, 1987), we thought it would be important to document marsh foraminifera in Japan where major earthquakes have caused significant coastal changes (Ota, 1992). Marsh foraminiferal zonations may prove useful in helping to define periodicity of large earthquakes in fossil deposits even though there are presently few living marshes existing on the mainland of Japan.

Previous work

As discussed above, Japanese workers have done a large body of work over the last 100 years. The best summary of these works is either in Takayanagi and Hasegawa (1987) or Nomura (1982). Scott *et al.* (in press) have summarized all the Pacific Rim marsh studies, including the data in this paper, and compared marsh foraminiferal assemblages around the Pacific Rim with those in the Atlantic.

At the time we sampled this marsh, a group led by M. Umitsu (Nagoya University) was also working in this marsh studying diatoms, but we are unaware of any published work from these studies yet.

In terms of overall marsh distribution, Ito *et al.* (1982) produced a complete vegetation map of Hokkaido which we used to locate our sample sites.

Physiography of wetland areas

These salt marshes are located on the eastern tip of Hokkaido inside Nemuro Bay in the Furen Lagoon (Figure 1). The marshes we sampled were on the inside upper part of Nemuro Bay and had restricted connection to the

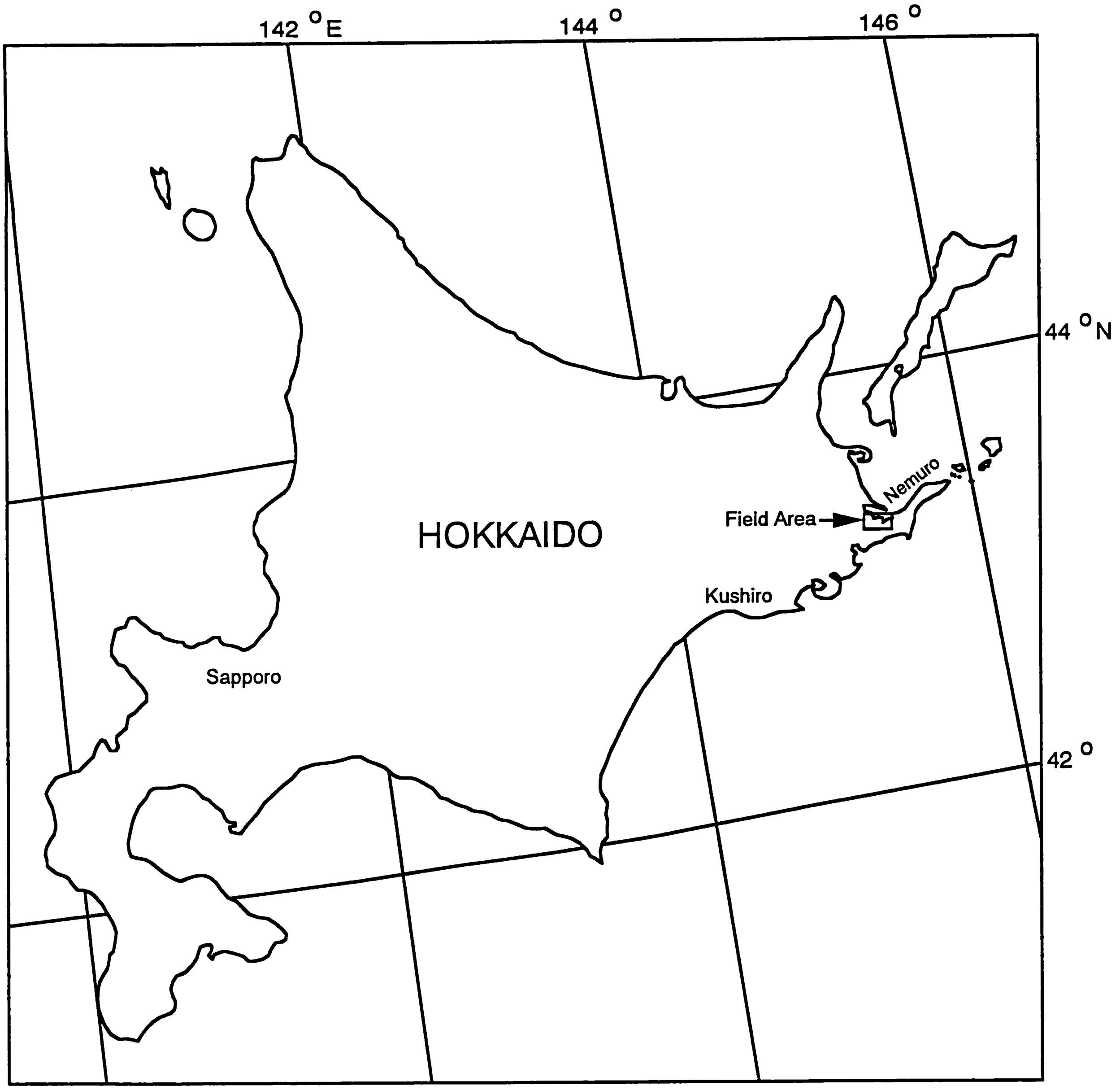


Figure 1. Regional map of Hokkaido, northern Japan with the area of Nemuro Bay indicated.

ocean. Although they are tidal, they are almost exclusively freshwater (see vegetation section). We did not measure salinities at the time, but Hasegawa returned this area in the winter of 1995 and measured salinities of 2.0‰ (trans. 1, stn. 1, at lowest marsh), 3.3‰ (6.3 m from stn. 1 in transect 2), 16.9‰ (stn. 1, transect 2), and 16.8‰ (stn 14 in transect 2). These readings were done under ice, so they would be different than summer values. Tidal ranges at nearby Kushiro are 0.5 m to 0.8 m (spring) and 0.2 m to 0.3 m (neap). Transect 1 (Figure 2) was the most open of the two transects, being located on a large channel that opens into Nemuro Bay but transect 2 was positioned at the head of a long channel and was almost at the mouth of the small creek that fed into the area. There were more marine marshes on the outer edge of Nemuro Bay but these were inaccessible to us in the time we had available.

Methods

Samples were collected with a small 3.5 cm diameter corer-only the upper 1 cm of sediment was collected to obtain a 10 cm^3 sample.

Material was wet sieved within one week using a .063 mm sieve (mesh 230) as the lower size to retain foraminifera and 0.5 mm as the upper size to catch roots and large plant fragments. Samples were preserved in buffered formalin and Rose Bengal (to detect living specimens).

Samples were retained in liquid suspension and examined in liquid under a dissecting microscope (20 to 40×). Large samples were split to aliquots of 300-500 specimens using a modified plankton splitter (Scott and Hermelin, 1993).

Organic material was not decanted away as in some earlier studies (e.g., Scott and Medioli, 1980); in some cases, most of the living specimens would have been washed away by decanting.

Photos of specimens were taken on a Bausch-Lomb scanning electron microscope in the Biology Department at Dalhousie. Plus-x 35 mm film was used.

Vegetation

Gnerally all the dominant plants were freshwater plants with some small occurrences of common marsh plants such as *Potentilla* sp., *Glaux maritima* and *Triglochin maritima.*

Some of the freshwater species are known from brackish marshes elsewhere (*Eleocharis* in marshes of the Mississippi Delta, Scott *et al.*, 1991) so it is not too surprising to see them in what was a tidal situation in the Hokkaido marshes. Because of access problems, we were not able to sample the more saline marshes in the outer part of Nemuro Bay (Figure 4) but only upper estuarine areas on the inner part of the Bay (Figures 2, 3).

Transect 1: Characteristic of extremely brackish marshes like this (e.g. brackish marshes in Louisiana, Scott *et al.* 1991), vegetation patterns followed almost no pattern with elevation as do saline marshes (Table 1, Figure 4). *Eleocharis kamchatica* was dominant in both the lowest and highest parts of this transect, with varying amounts of *Scirpus, Juncus, Carex*, and low percentages of *Potentilla*. The only vertical zonation is that trees and upland plants are restricted to the upper marsh.

Transect 2: This transect is similar to transect 1 except that the lowest marsh is dominated by *Carex*, not *Eleocharis*, while the highest marsh is again dominated by *Eleocharis* (Table 1, Figure 5). The plant diversity of this transect is higher than in transect 1, notably containing traces of more true salt marsh plants (*Glaux* and *Triglochin*) as well as more *Scirpus* species. Again the only notable veritcal zonation is in the upper marsh where trees and other upland plants come in.

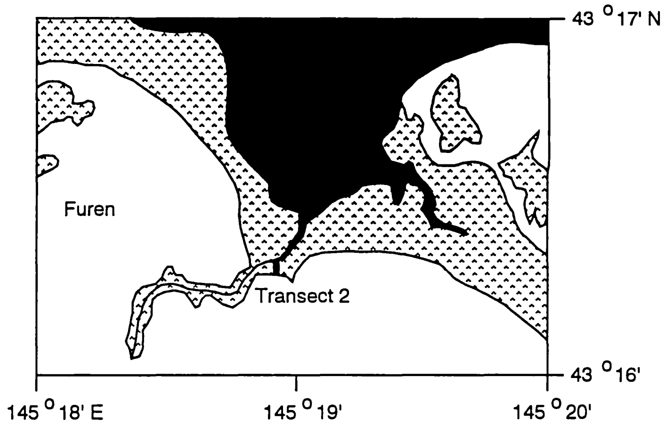


Figure 3. Location of Transect 2. Note coordinates.

Foraminifera

In keeping with the brackish nature of this marsh, the foraminiferal diversity is very low here, and there are poorly developed vertical zones (Tables 2, 3, Figures 4, 5).

Transect 1: This transect was the longer of the two transects with 31 sample locations (Tables 1, 2, Figures 2, 4). Sampling for foraminifera started just below the lowest plants and continued into the tree line. In stations 1-20, *Miliammina fusca* was the most abundant overall, alternating occasionally with *Trochammina macrescens* f. *macrescens.* Living populations follow total abundances of *T. macrescens* with greatest numbers of living specimens usually being dominated by *T. macrescens.* There are some very high numbers of living specimens at some stations (e.g. Stns. 3, 10 and 23, with over 10,000 living in a 10 cc sample) and these living populations are invariably dominated by *T. macrescens.* From Station 21 to 29, the

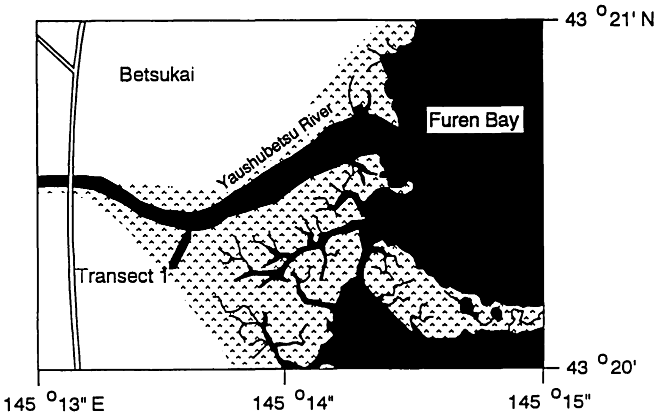


Figure 2. Location of Transect 1. Note coordinates.

Table 1. Vegetation distributions for Transects 1 and 2.

Transect 1		Transect 2	
Stations 1-5 :	50%-80% *Eleocharis kamchatica* 20%-50% *Scirpus* sp. (Station 5 has traces of *Juncus* and *Potentilla*)	Stations 1-3 :	85% *Carex subspathacea* 10% *Eleocharis kamchatica* plus *Triglochin maritima* and *Potentilla* (5%)
		Stations 4, 5 :	50%-80% *Calamagrantis epigeious* 15%-50% *C. subspathacea*
Stations 6-9 :	30%-100% *Carex subspathacea* with varying %'s of *Scirpus, Potentilla, E. kamchatica* (station 6 only), and *Juncus*	Stations 6-10 :	50%-95% *C. subspathacea* 5%-10% *E. kamchatica* with *Glaux maritima Potentilla* sp. and *Scirpus* sp. also occurring
Station 10 :	50% *E. kamchatica* 40% *Scirpus* sp. 10% *Juncus* sp. Trace *Potentilla* sp.		
Stations 11, 12 :	50% *Scirpus* 50% *Juncus*	Stations 11, 12 :	40%-50% *C. subspathacea* 15%-50% *Scirpus* sp. plus some *E. kamchatica* and *Carex epigeious*
Stations 13-20 :	0%-60% *Scirpus takemaemontani* 0%-30% *E. kamchatica* 10%-100% *Juncus* (100% at Stn. 16) 0%-50% *Scirpus* sp. 0%-50% *Potentilla* sp. Stn. 18 end of *Juncus* ; First dead trees at Stn. 19	Stations 13, 14 :	100% *Scirpus* sp. and *S. takemaemontani*
		Stations 15, 16 :	10%-50% *C. subspathacea* 20%-40% *E. kamchatica* plus *Poamacrocalyx trautu, Potentilla, Stellaria humifusca, Miscanthus sinensis*
Stations 21-23 :	85%-95% *E. kamchatica* 5%-15% *Potentilla* Plus some Upland Plants ; Sediment dry	Stations 17, 18 :	50%-90% *E. kamchatica* 10%-50% Upland Plants
		Station 19 :	100% Upland Plants
Station 24 :	25% *E. kamchatica* 70% *Scirpus* 5% *Potentilla*		
Stations 25-31 :	25%-90% *E. kamchatica* plus *Scirpus*, etc. and Upland Plants ; Edge of Forest at Stn. 31		

fauna changes to one dominated by *T. macrescens* and *Haplophragmoides manilaensis* with *M. fusca* still being common. At Stations 30 and 31, the fauna becomes freshwater, dominated by *Centropyxis aculeata* ; this fauna has low living numbers, as well as lower totals. Overall total numbers vary from 2 to 19,872/10 cc with living varying from 0 to 10,908/10 cc.

Transect 2 : This transect was shorter and in a more restricted area than transect 1 (Tables 1, 2, Figures. 3, 5). This is reflected in the foraminiferal fauna which is dominated by *T. macrescens* throughout its length up to Station 16 where *H. manilaensis* becomes prominent. Above Station 16, *C. aculeata* is dominant as the upland plant zone is reached. Together with the dominance of *T. macrescens*, numbers of living specimens are generally higher and fluctuate less than in transect 1. Overall total numbers are also higher with three stations having over 20,000 individ./10 cc. Ranges are 1 to 9776 individ./10 cc for living and 342 to 27,968 individ./10 cc for total populations.

Comparison with other marsh areas

The species diversity in the Hokkaido marshes is much lower than other marsh areas that have been reported, even those with lowered salinities. Several species that might have been expected such as *Ammotium salsum, Tiphotrocha comprimata, Ammostauta inepta, Ammobaculites* spp., and *Haplophragmoides wilberti* are either not present or rare. These have been reported in other brackish marshes (Scott and Medioli, 1980 ; Scott *et al.*, 1990, 1991) but are not here. Scott *et al.* (in press) note that some of these species (*T. comprimata, A.inepta* and *H. wilberti*) are not common in any Pacific Rim marshes, possibly as a result of being away from the main migratory waterfowl flyways which are probably the most important dispersement mechanisms for marsh foraminifera. However, the Hokkaido marshes are even more isolated, lacking the common Pacific species such as *A. salsum*. One reason for this might be the general absence of salt marsh wetlands in Japan as a whole which would attract less waterfowl although the nearby Kushiro area does have a substantial freshwater wetland

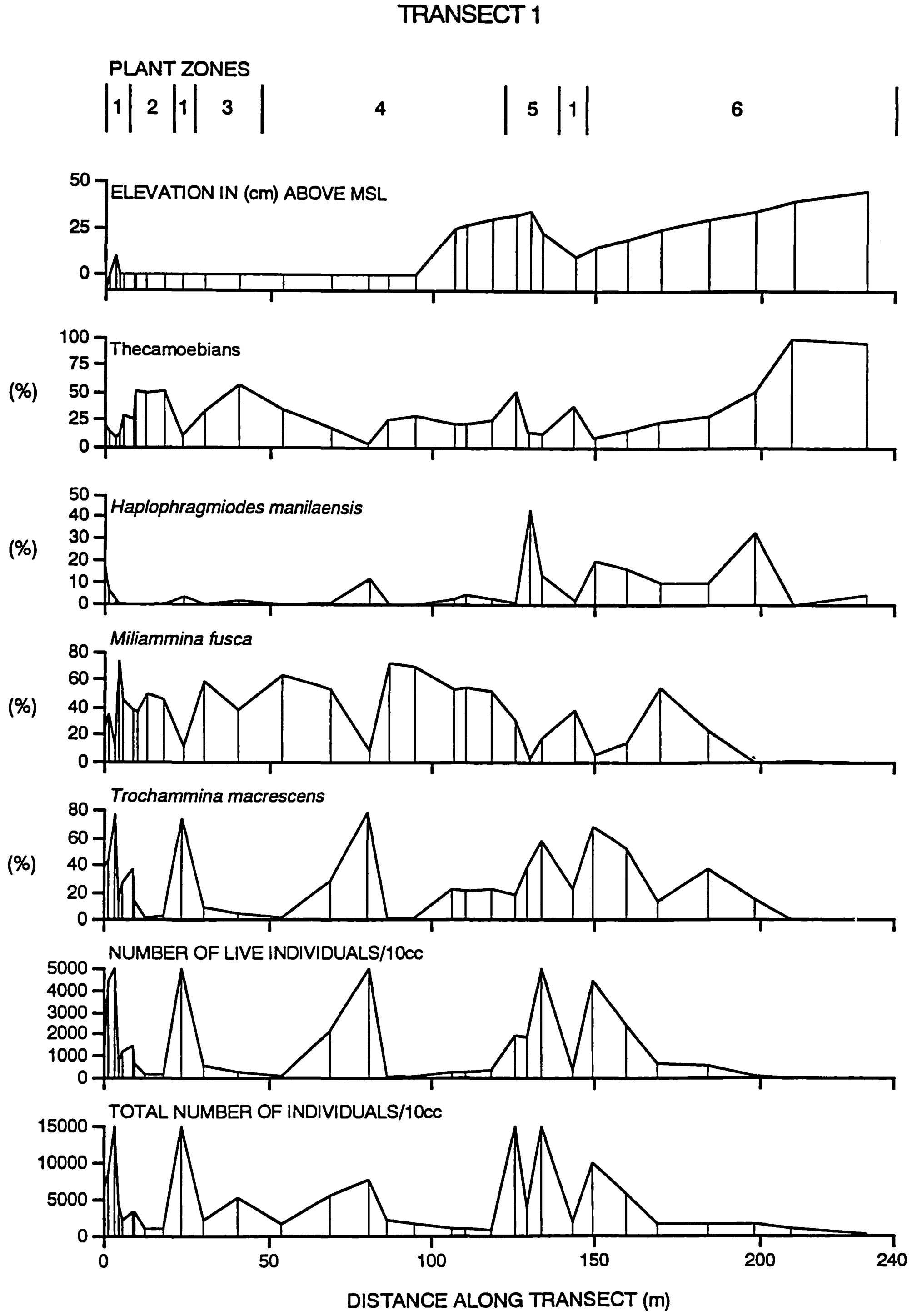


Figure 4. Foraminiferal and vegetation distributions along Transect 1. Elevations shown are approximate-they are based on .8 m spring tide range with higher high water at the treeline. Vegetation is detailed in Table 1 and foraminiferal data in Table 2. Vegetation zones by number: 1) *Eleocharis/Scirpus*, 2) *Carex* + others, 3) *Scirpus, Juncus*, 4) *S. takemaemontani* + others (first tree at Stn. 19), 5) *Eleocharis* + upland plants, dry soil, 6) *Eleocharis* + others + upland (forest starts at Stn. 31)

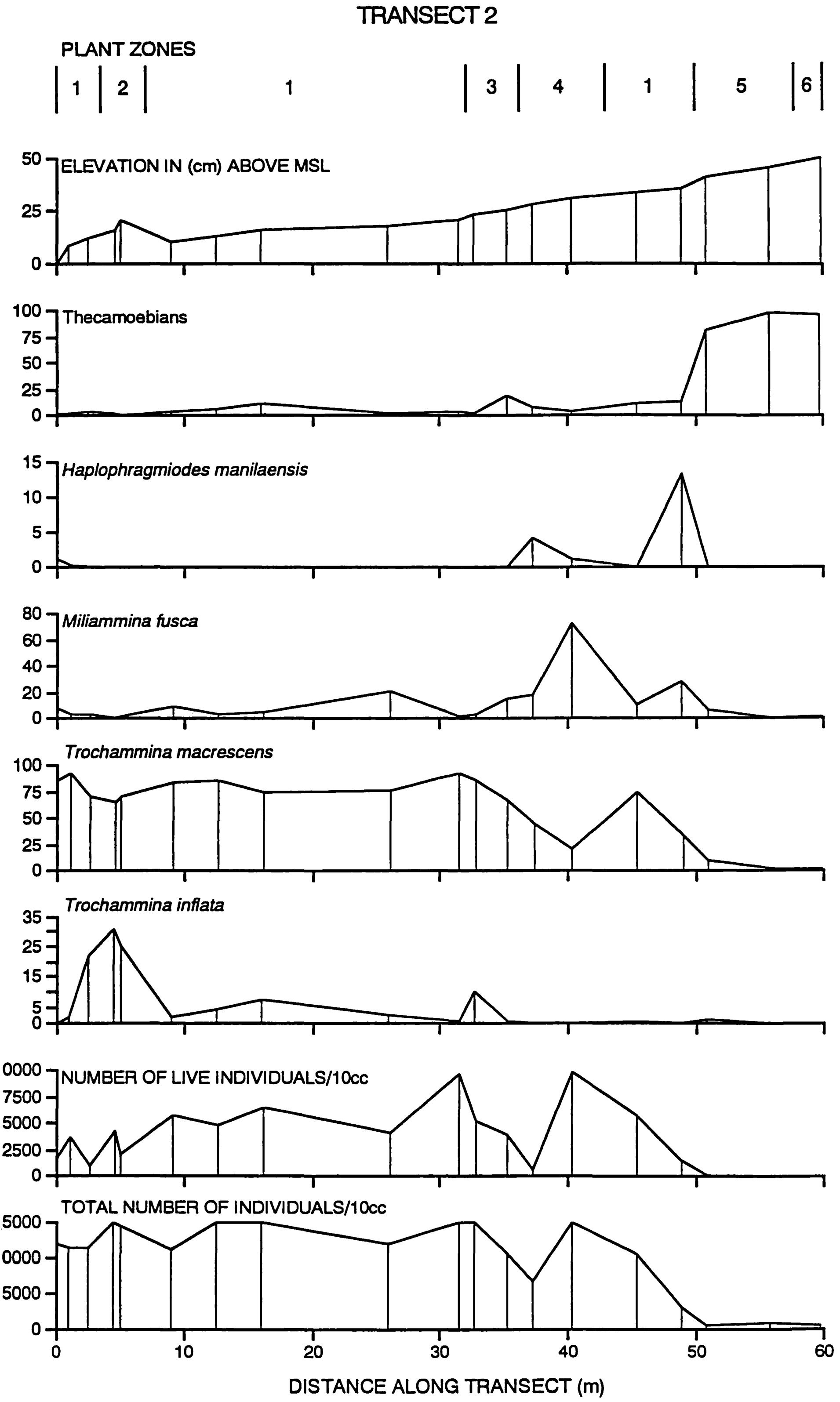


Figure 5. Foraminiferal and vegetation distributions along transect 2. Elevations shown are as for Transect 1. Vegetation is detailed in Table 1 and foraminifera in Table 3. Vegetation zones are as follows: 1) *Carex/Eleocharis*, 2) *Calamagrantis*/Carex, 3) *Carex/Scirpus*, 4) *Scirpus*, 5) *Eleocharis*/upland, 6) upland plants.

Table 2. Foraminiferal abundances and relative percentages for

STATION NUMBER	1		2		3		4		5		6	
ELEVATION cm ABOVE MSL	−15		0		20		0		0		0	
DISTANCE ALONG TRANSECT (m)	0		0.5		1		1.5		5.5		8.5	
(live/total)	L	T	L	T	L	T	L	T	L	T	L	T
NO. OF SPECIES	4	7	4	5	4	4	3	5	3	4	3	3
NO. OF INDIVIDUALS	1314	6588	4464	8688	10896	16872	752	4512	1176	2296	1520	3448
Ammobaculites exiguus												
Haplophragmoides manilaensis	5.5	17.2	4.3	6.1	1.1	2.4						
Miliammina fusca	32.9	24.0	33.3	34.3	8.4	11.8	55.3	73.0	40.8	44.6	32.1	38.5
Pseudothurammina limnetis				2.2						0.3		
Tiphotrocha comprimata		0.5										
Trochammina inflata		0.3										
T. macrescens f. *macrescens*	56.2	38.3	60.2	43.1	89.4	76.8	42.6	14.5	49.0	27.2	63.2	37.4
T. macrescens f. *polystoma*		0.3										
Planktonics								0.4				
Centropyxis aculeata	5.5	19.4	2.2	14.4	1.1	9.0	2.1	11.3	10.2	27.9	4.7	24.1
C. constricta												
Difflugia oblonga								0.7				
D. proteiformis												
Nebella collaris												
Tinnitinnopsis rioplatensis												

STATION NUMBER	17		18		19		20		21		22	
ELEVATION cm ABOVE MSL	0		50		55		60		65		70	
DISTANCE ALONG TRANSECT (m)	94.5		106.5		110.5		118.5		125.5		129.5	
(live/total)	L	T	L	T	L	T	L	T	L	T	L	T
NO. OF SPECIES	3	3	4	5	4	5	4	4	3	4	4	5
NO. OF INDIVIDUALS	104	1680	276	1048	316	1012	336	844	1908	15840	1896	3996
Ammobaculites exiguus						0.4						
Haplophragmoides manilaensis			1.4	1.9	3.8	4.0	1.2	1.9		0.9	35.4	42.9
Miliammina fusca	46.2	68.6	43.5	52.7	45.6	53.8	47.6	51.7	9.4	29.8		1.8
Pseudothurammina limnetis											0.6	1.2
Tiphotrocha comprimata												
Trochammina inflata												
T. macrescens f. *macrescens*	30.8	1.9	52.2	23.3	44.3	20.9	29.8	22.3	64.2	17.7	62.7	39.6
T. macrescens f. *polystoma*												
Planktonics												
Centropyxis aculeata	23.1	29.5	2.9	21.4	6.3	20.9	21.4	24.2	26.4	51.6	1.3	14.4
C. constricta												
Difflugia oblonga				0.8								
D. proteiformis												
Nebella collaris												
Tinnitinnopsis rioplatensis												

Transect 1. Also shown are elevation (not accurate) and distance along transect.

7		8		9		10		11		12		13		14		15		16	
0		0		0		0		0		0		0		0		0		0	
9.5		12.5		17.5		23.5		30		40		53.5		68.5		80.5		86.5	
L	T	L	T	L	T	L	T	L	T	L	T	L	T	L	T	L	T	L	T
3	4	3	5	3	3	5	5	3	5	3	5	2	4	4	6	4	4	3	5
680	3216	152	1224	200	1060	10752	17280	584	2256	272	5280	104	1688	2160	5568	5808	7728	88	2176
											0.6								0.4
						0.9	3.1				1.2				0.6	9.4	11.2		
30.6	36.3	73.3	49.3	84.0	45.3	9.4	11.7	63.0	57.8	70.6	37.9	76.9	62.6	28.1	53.2	5.5	7.7	63.6	72.1
						0.4	0.6		0.4					0.7	0.3				
49.4	13.2	15.8	2.3	12.0	3.4	87.1	74.4	31.5	9.9	23.5	4.5	23.1	2.4	65.2	28.2	84.8	78.9	9.1	1.8
20.0	50.2	10.5	47.7	4.0	51.3	2.2	10.3	5.5	31.6	5.9	55.8		33.6	5.9	17.5	0.3	2.3	27.3	25.4
			0.3																
	0.2		0.3										1.4						0.4
															0.3				
									0.4										

23		24		25		26		27		28		29		30		31	
45		20		30		40		50		60		70		80		90	
133.5		143.5		149.5		159.5		169.5		184.5		198.5		209.5		231.5	
L	T	L	T	L	T	L	T	L	T	L	T	L	T	L	T	L	T
4	4	3	4	4	4	4	5	4	5	4	5	3	4	2	5	0	2
10908	19872	416	1872	4480	10000	2416	5968	688	1584	520	1704	136	1656	32	1240	0	384
10.9	13.0	3.8	1.7	17.1	19.5	13.2	18.6	2.3	10.1	6.2	9.9	52.9	33.3				4.2
6.6	16.8	42.3	38.5	2.1	4.6	13.9	14.5	77.9	54.0	18.5	23.5				0.6		
							0.3							0.5			
81.8	58.0	53.8	22.2	76.4	68.2	68.2	52.8	16.3	13.1	67.7	37.6	29.4	15.0				
0.7	12.1		37.6	4.3	7.7	4.6	15.8	3.5	22.2	7.7	28.6	17.6	51.2	25.0	94.8		95.8
									0.5		0.5				1.9		
															0.6		
														75.0	1.9		

Table 3. Foraminiferal abundances and relative percentages for

STATION NUMBER	1		2		3		4	
ELEVATION IN cm ABOVE MSL	0		15		23		31	
DISTANCE ALONG TRANSECT (m)	0		1		2.5		4.5	
(live/total)	L	T	L	T	L	T	L	T
NO. OF SPECIES	4	8	3	6	2	7	3	6
NO. OF INDIVIDUALS	1632	11712	3792	11216	944	11312	4224	27968
Ammobaculites exiguus		0.8				0.4		
Haplophragmoides manilaensis	2.0	1.1		0.4				
Miliammina fusca	3.9	7.1	2.5	3.1		3.5	1.5	0.2
Polysaccammina ipohalina								
Pseudothurammina limnetis								0.7
Quinqueloculina seminulum								
Tiphotrocha comprimata						0.3		0.5
Trochammina inflata			2.1	1.4	11.9	21.5	36.4	31.1
T. macrescens f. *macrescens*	93.1	86.2	95.4	92.9	88.1	71.0	62.1	65.2
T. macrescens f. *polystoma*								
Centropyxis aculeata		1.2		1.6		1.8	2.3	
C. constricta		0.3		0.6		1.4		
Difflugia globulus								
D. proteiformis								
Lesquereusia spiralis								
Nebella collaris								
Ammonia beccarii		0.3						
Trochammina inflata (sipho-type)	1.0	3.0						

STATION NUMBER	11		12		13		14	
ELEVATION IN cm ABOVE MSL	45		50		55		60	
DISTANCE ALONG TRANSECT (m)	32.8		35.3		37.3		40.3	
(live/total)	L	T	L	T	L	T	L	T
NO. OF SPECIES	3	5	4	5	4	6	5	5
NO. OF INDIVIDUALS	5136	16736	3904	10304	596	6454	9776	16064
Ammobaculites exiguus					50.0	24.8	2.0	3.2
Haplophragmoides manilaensis						4.3	0.3	1.0
Miliammina fusca	2.2	2.4	5.7	14.9	28.6	18.2	78.4	72.2
Polysaccammina ipohalina								
Pseudothurammina limnetis								
Quinqueloculina seminulum								
Tiphotrocha comprimata								
Trochammina inflata	8.7	10.0		0.3				
T. macrescens f. *macrescens*	89.1	85.1	91.8	67.1	14.3	45.5	18.7	20.8
T. macrescens f. *polystoma*								
Centropyxis aculeata		2.1	0.8	13.0		5.6	0.7	2.8
C. constricta		0.4	1.6	4.7	7.1	1.7		
Difflugia globulus								
D. proteiformis								
Lesquereusia spiralis								
Nebella collaris								
Ammonia beccarii								
Trochammina inflata (sipho-type)								

Transect 2. Also shown are elevations (not accurate) and distance along transect.

5		6		7		8		9		10	
40		20		25		30		35		40	
5		9		12.5		16		26		31.5	
L	T	L	T	L	T	L	T	L	T	L	T
2	5	7	7	3	7	3	6	4	7	2	4
2048	14272	5776	11056	4864	25344	6528	31872	4032	11856	9664	21120
	0.9	0.3	0.3		0.3	1.0	2.8		0.7		
	2.2	2.5	9.0	1.3	3.3		4.4	8.3	20.1	2.0	1.8
									0.1		
	0.4	0.3	0.3		0.3						
		0.3	0.1					0.4	0.1		
28.1	25.1	1.4	1.6	2.6	4.5	10.8	7.6	1.2	2.3		0.6
71.9	71.3	95.0	84.5	96.1	86.4	88.2	74.1	90.1	75.6	98.0	93.0
		0.3	4.2		5.1		10.2		1.1		4.5
					0.3		0.8				

15		16		17		18		19	
65		70		80		90		100	
45.3		48.8		50.8		55.8		59.8	
L	T	L	T	L	T	L	T	L	T
3	6	6	6	3	6	1	4	1	5
5664	10464	1400	2976	66	498	6	828	72	342
					1.2				
		5.1	13.4						
5.9	10.6	40.0	28.2	27.3	6.0				1.8
	3.7	9.7	11.8		1.2				
	0.5				1.2				
93.2	73.9	42.3	33.3	54.5	9.6		1.4		1.8
		0.6	0.3						
0.8	11.0	2.3	12.9	18.2	80.7	100	97.1		63.2
									1.8
	0.5								
							0.7		
							0.7	100	31.6

system.

Vertical zonation of marsh foraminiferal assemblages is also weak here; however *Haplophragmoides manilaensis* does occur mostly in the higher elevations as it does in other locations (Scott and Medioli, 1980; Collins *et al.*, 1995). Lack of well defined zonations was also observed in the Louisiana brackish marshes where salinities were less than 10‰ and plant species were largely freshwater species as they are here (Scott *et al.*, 1991). However it is important to note that there is a clear delineation in Hokkaido between the upland and highest marsh as there is in every other reported marsh situation.

Discussion

To our knowledge, this is the first study of recent marsh foraminifera in Japan; this may in part be due to the total lack of marshes in Japan except for the ones we sampled in Nemuro Bay. This is also ignoring any work done in Okinawa on marsh-mangrove systems. However, although there are very few marshes in Japan presently, presumably there were extensive marsh systems in the past before they were reclaimed for agriculture and residential purposes over the last few hundred years. Hence it is important to know what foraminiferal species to expect if core or drillhole material in coastal deposits has salt marsh peats incorporated into the section. As in other areas, the foraminiferal zones can be used to accurately relocate former sea levels although in these brackish marshes the zonation is not as accurate as in normal marine marshes. However it is possible to differentiate tidal marshes from freshwater marshes simply with the presence of large numbers of foraminifera, something that would not be possible by looking at plants only.

With marsh foraminifera as a tool, it may be possible to look at coastal deposits in Japan with respect to determining rapid base level changes that result from earthquakes. This technique is already being applied in the United States and Canada (e.g. Atwater, 1987; Jennings and Nelson, 1992). Atwater has actually suggested a periodicity for major quakes in the Washington State coastline and similar techniques might be very useful to coastal planners in Japan.

Systematic taxonomy

For generic distinctions, we follow Loeblich and Tappan (1964, 1987). Only the original references are listed here.

Ammobaculites exiguus (Cushman and Brönnimann)

Figure 6-1

Ammobaculites exiguus Cushman and Brönnimann, 1948, p. 38, pl. 7, figs. 7, 8.

Ammobaculites dilatatus Cushman and Brönnimann. Scott and Medioli, 1980, p. 39, pl. 1, figs. 6-8.

Centropyxis aculeata (Ehrenberg)

Figure 6-9

Arcella aculeata Ehrenberg, 1832, p. 91.

Centropyxis aculeata (Ehrenberg). Stein, 1859, p. 43.

Haplophragmoides manilaensis Andersen

Figure 6-3, 4

Haplophragmoides manilaensis Andersen, 1953, p. 22, pl. 4, fig. 8

Haplophragmoides bonplandi Todd and Brönnimann, 1957, p. 23, pl. 2, fig. 2: Scott and Medioli, 1980, p. 40, pl. 2, figs. 4, 5.

Miliammina fusca (Brady)

Quinqueloculina fusca Brady, 1870, p. 47, pl. 11, figs. 2, 3.

Miliammina fusca (Brady). Phleger and Walton, 1950, p. 280, pl. 1, figs. 19a, b.

We did not illustrate this species since it has been reported several times before from Japan (e.g., Takayanagi, 1955).

Nebela collaris (Ehrenberg)

Figure 6-5

Difflugia collaris Ehrenberg, 1848, p. 218.

Nebela collaris (Ehrenberg). Leidy, 1879, p. 145, 146, pl. 22, pl. 23, figs. 1-7, pl. 24, figs. 11, 12.

Pseudothurammina limnetis (Scott and Medioli)

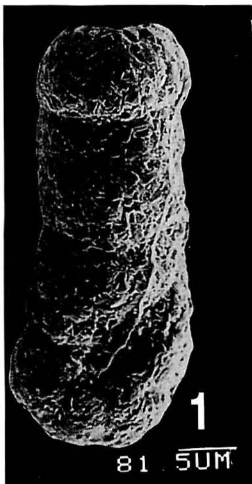
Figure 6. 2

Astrammina sphaerica (Heron-Allen and Earland). Zaninetti *et al.*, 1977, pl. 1, fig. 9

Thurammina ? limnetis Scott and Medioli, 1980, p. 43, 44, pl. 1, figs. 1-3.

Pseudothurammina limnetis (Scott and Medioli). Scott, Medioli and Williamson, *In* Scott *et al.*, 1981, p. 126, 127.

Figure 6. Scale bars are by each specimen. **1.** *Ammobaculites exiguus* (Cushman and Brönnimann), *side view.* **2.** *Pseudothurammina limnetis* (Scott and Medioli), side view. **3, 4.** *Haplophragmoides manilaensis* Andersen, 3: Side view, 4: Edge aperture view. **5.** *Nobella collaris* (Ehrenberg), side view. **6-8.** *Trochammina macrescens* Brady, 6: f. *macrescens*, ventral, 7: f. *polystoma*, ventral, 8: dorsal. **9.** *Centropyxis aculeata* (Ehrenberg), side view. **10-17.** *Trochammina inflata* (Montagu), 10: Regular *T. inflata*, dorsal, 11: "Sipho" type, dorsal, 12: Regular *T. inflata*, ventral, 13-17: "Sipho" types, ventral showing various degrees of "Sipho" aperture from strongly developed (Figures 16, 17) to less developed (Figures 14, 15). Except for test composition, specimen 14 would be indistinguishable from "regular" *T. inflata* (Figure 12).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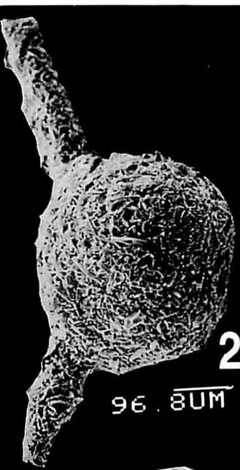
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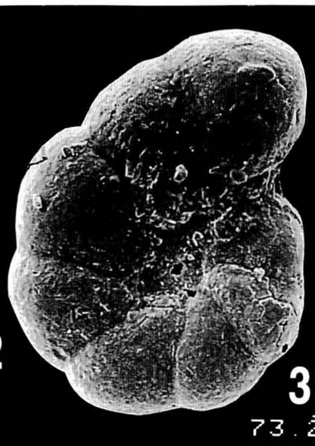
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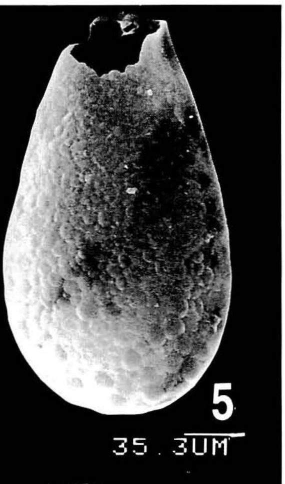
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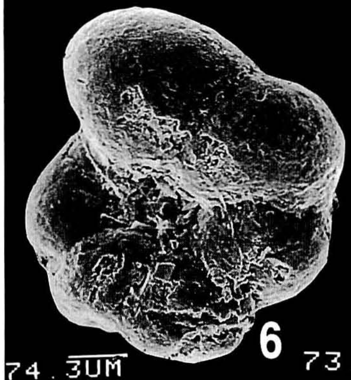
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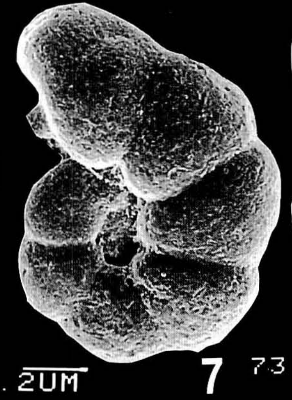
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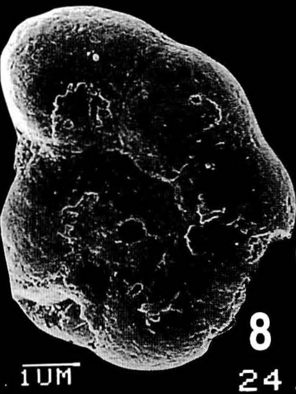
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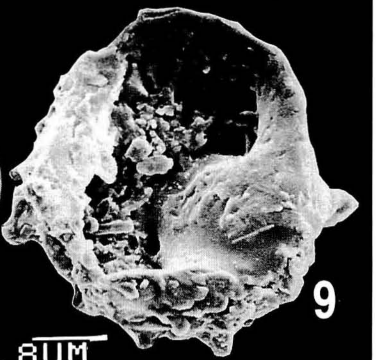
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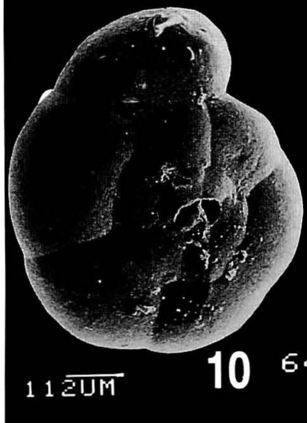
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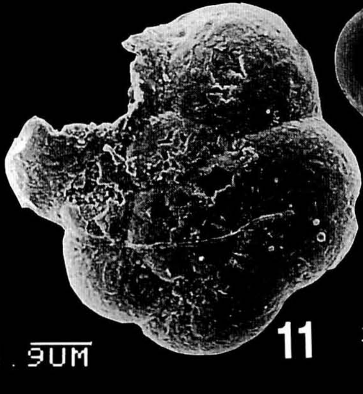
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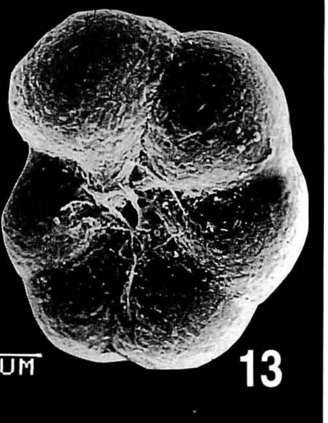
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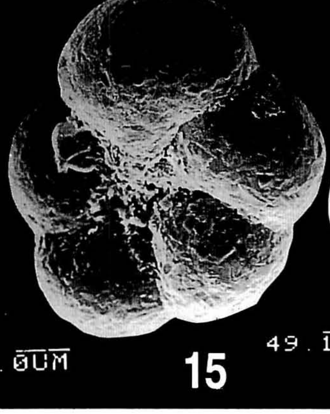
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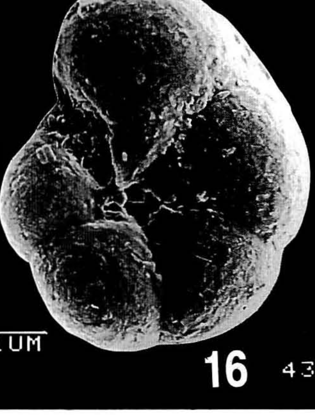
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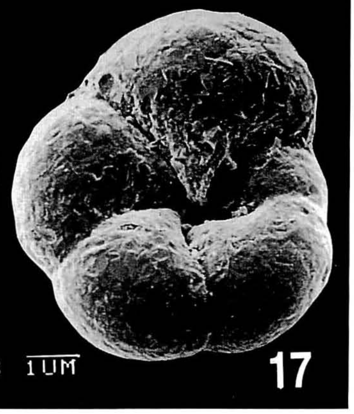
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Trochammina inflata (Montagu)

Figure 6-10—17

Nautilus inflata Montagu, 1808, p. 81, pl. 18, fig. 3.
Trochammina inflata (Montagu). Parker and Jones, 1859, p. 347.

Illustrations here include "Sipho" type *T. inflata* (Figures 11, 13-17) which have an extended aperture into the umbilical area. We show a range of specimens here which we believe shows the intergradation into *T. inflata* (Figures 10, 12). Also note the smaller size of the "Sipho" types; the texture and size are reminiscent of the microspheric *T. inflata* reported in Scott and Medioli (1980).

Trochammina macrescens Brady

Figures 6-6—8

Trochammina inflata (Montagu) var. *macrescens* Brady, 1870, p. 240, pl. 11, figs. 5a-c.
Jadammina polystoma Bartenstein and Brand, 1938, p. 381, figs. 1a-c, 2a-1.
Trochammina macrescens Brady. Phleger and Walton, 1950, p. 281, pl. 2, figs. 6, 7.

This species includes two forms-forma *polystoma* (Figure 7) and forma *macrescens* (Figures 6, 8)-both of which are illustrated here. As Scott and Medioli (1980) show, the only difference between the two forms are absence or presence of supplementary apertures which appears to be a response to salinity. Forma *polystoma* is very rare in these Hokkaido marshes.

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1000 "Shelly softground" colonized by an endobyssate bivalve, *Modiolus kurilensis*: an example of taphonomic feedback from the Pleistocene of Kanazawa, Japan

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Abstract. Colonization by an endobyssate bivalve *Modiolus kurilensis* was possible only in shelly softground conditions, that is, on a soft bottom with the shells being slightly buried with fine sediment. The Pleistocene Omma Formation, Kanazawa, generally exhibits a shelly bottom carpeted by shells (shell pavement) or a shelly bottom covered by soft sediment too thick to allow colonization by *Modiolus*. The described *Modiolus* colony was found in the lower unit of the Omma Formation, where sealevel change was relatively small and where shelly softground conditions were present. In contrast, *Modiolus* is much less common in the shell beds in the cyclothemic middle unit of the formation. An important environmental factor accounting for the uncommon occurrence of *Modiolus* in cycle-bounding shell beds is their repeated physical reworking followed by deposition of soft sediment too thick to be colonized by *Modiolus*.

Key words: Shelly softground, taphonomic feedback, bivalve, *Modiolus kurilensis, Modiolus modiolus difficilis,* Omma Formation, Pleistocene

Introduction

This note originated from a find of a well-preserved endobyssate bivalve colony underlain by a shell lens in the early Pleistocene Omma Formation. Establishment of the bivalve colony described herein was most probably facilitated by the presence of shell material on an otherwise barren silty sand bottom which was difficult for endobyssate bivalves to colonize. In our experience, gregarious colonies of endobyssate bivalves are not uncommon, an example being those found in the Pleistocene Jizodo Formation, Boso Peninsula. There is, however, no published taphonomical and paleoecological description of such bivalve colonies. Taphonomically similar examples have been studied by Ziegler *et al.* (1966), Walker and Parker (1976), Johnson (1977) and Wilson (1982), but for much older Paleozoic brachiopod colonies.

Kidwell and Jablonski (1983) proposed a concept of taphonomic feedback for such fossil occurrences, whereby dead hardparts facilitate or inhibit the colonization of a subsequent community. They used the term taphonomic to emphasize the postmortem processes that figure in the availability of dead hardparts, and the term feedback to emphasize that not only does the life assemblage influence the death assemblage (as in conventional taphonomy), but the death assemblage in turn affects the life assemblages. The concept of taphonomic feedback is distinguished from "ecological succession" in emphasizing that not only living organisms but also dead hardparts influence subsequent life assemblages. Recognition and description of such taphonomic feedback are actually common in earlier studies of modern communities or fossil assemblages. For example, as early as the 1930's, Powell (1937) discussed substratum modification by accumulating shell and its effect on the distribution of marine benthic communities in his study of animal communities in Auckland Harbor in New Zealand. As an ancient example, Aigner (1982) discussed modified substratum conditions as an inferred consequence of high-energy events in Triassic shallow marine deposits of Southwest Germany, and classified them under softground, firmground and hardground.

Kidwell (1989) thoroughly reviewed the literature describing taphonomic feedback from ancient and modern marine environments. Also, she tested taphonomic feedback in thick shell beds in the Miocene of Maryland, by examining relative abundance of shell-gravel dwellers and shell content in the sediments, and concluded that the correlation between them was statistically significant.

This paper describes a simpler, but unambiguous example of taphonomic feedback which acted to establish a colony of an endobyssate bivalve in a shallow-marine environment in the Early Pleistocene of Japan. We also discuss a characteristic substratum condition termed a shelly softground.

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Geologic setting and observation

The bivalve colony was found at the type locality of the Early Pleistocene Omma Formation, along the River Saikawa in a suburb of Kanazawa City, on the Japan Sea coast of central Japan. The Omma Formation is about 200 m thick, and is characterized by at least ten shell-bed bounded sedimentary cycles, which originated from early Pleistocene glacio-eustatic sea-level changes (Kitamura and Kondo, 1990; Kitamura *et al*. 1994). The middle, cyclic part of the Omma Formation comprises alternating shallow (upper sublittoral) and deep (lower sublittoral) molluscan fossil associations. Also, most of the species in the upper sublittoral associations are cold sea type and all the constituents of the lower sublittoral associations are warm sea type, common in the Kuroshio. Such linked changes between water depth and marine climate clearly suggest a glacio-eustatic origin for the cyclic environmental change. In contrast, the lower unit of the formation consists of relatively monotonous bluish-gray, partly brown, fine-grained sandstone with sporadic mollusc and echinoid remains and occasional shell lenses consisting of articulated or disarticulated valves of *Anadara amicula*. The *Modiolus* colony was preserved resting on one of these shell lenses, stratigraphically located 2.5 m above SB3 (fig. 5, Kitamura, 1991a). In the upper transitional unit to the middle unit of the Omma Formation, dense shell beds showing characteristics of stormy condition are present (Kitamura, 1991a). The inferred depositional environment for most of the lower unit is upper sublittoral, within a cold-water oceanographic regime.

A concretionary block sample containing the bivalve colony and of 40×50×20 cm size was extracted, and biostratinomic observation of shell orientation and disarticulation ratio was made in the laboratory. The block sample is deposited in the Department of Geology, Kochi University.

Description of the colony and the underlying shell lens

Figure 1 shows horizontal and cross-sectional views of the bivalve colony. The bivalve is identified as a living species, *Modiolus kurilensis* Bernard 1983. The well-known synonyms include *Modiolus difficilis* and *Modiolus modiolus difficilis*, and the species is known as "ezohibarigai" in Japanese. Fossils of this species have been reported from the Pleistocene of South Kanto (Oyama, 1973, and many other papers), e.g. the Miyata Formation in the Miura Peninsula and the Jizodo, Yabu and Kiyokawa Formations in the Boso Peninsula, the Pleistocene of Hokuriku including Omma Formation (Kaseno and Matsuura, 1965), and the Pleistocene of Hokkaido (Sakagami *et al*. 1966; Suzuki, 1989). Lenticular concentrations of mostly unabraded shells of *Anadara amicula*, an extinct infaunal arcid bivalve, underlie the *Modiolus* colony. All the shell lenses are only one layer thick. Some of the shells are still articulated, but commonly they gape and are stacked with similar orientation or with opposed postures. No *in-situ* preserved *Anadara* specimen was found in this block (Figure 1), nor in other *Anadara* shell lenses. The shell lenses of *Anadara amicula* in the lower unit of the Omma Formation are, therefore, current-or wave-worked shell concentrations, rather than an *in-situ* occurrence, despite the presence of common articulated valves and well-preserved shells.

In the sampled block, two individuals (four valves) of *Anadara amicula* are articulated among 29 detached valves (disarticulation ratio is 86.2%; Figure 2). Shells of *M. kurilensis* are often found in the upper part of or just above the *Anadara* shell lenses. Thirty-three articulated specimens and nine detached valves were found. Many of the *Modiolus* shells in the block are preserved in life position with commissure planes roughly vertical and shell long axes inclined at 60-70 degrees to the bedding plane (Figure 3). The shell surfaces are pristine, with no encrustation or boring.

Lenticular shell concentrations of *Anadara amicula* are considered to have served as the stable substrata on which the *M. kurilensis* colony developed. The presence of *Anadara* shells made bottom scouring and resultant reworking less common, thereby permitting colonization by *Modiolus*. Just above the *Anadara* lens, both articulated and detached specimens of *Modiolus* are scattered through the sediment. Articulated specimens do not retain their life orientation, and post-mortem disturbance is inferred at this stage (Figure 4-II), which preceded formation of the gregarious colony. This is probably because the *Anadara* shells were almost exposed on the sea floor or only very shallowly buried, so that *Modiolus* individuals were easily reworked on the sea floor.

In the following stage (Figure 4-III), a well-developed colony consisting of about 20 individuals was established. Most of the individuals in the colony are preserved in life orientation, as described above. The underlying shell layer was buried to a depth of c. 5-6 cm when the colony was formed, as inferred from the stratigraphic distance

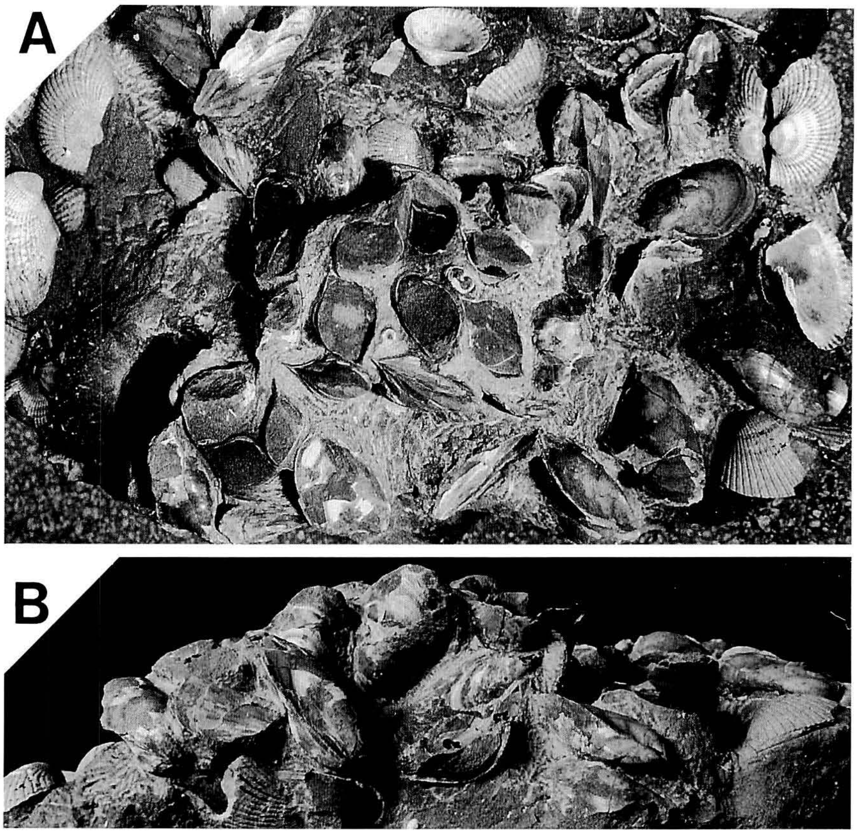

Figure 1. Photograph of the colony of *Modiolus kurilensis*. A : plan view. B : cross-sectional view. Scale : the width of the photograph is about 35 cm.

between the shell layer and the reconstructed sea floor surface from the preserved life positions. This colony did not, however, continue to grow further (Figure 4-IV). *Modiolus* shells do not appear to facilitate successive colonization of the animal, probably because of the physical instability of a colony which is only supported by byssal threads. This is a major structural and taphonomic difference with much stable, cement-attached bivalve colonies formed by bivalves such as oysters.

Several other shell lenses in the same horizon occur nearby to the colony studied here. These shell lenses consist similarly of *Anadara amicula* and *M. kurilensis*, but *Modiolus* specimens were mostly detached and we could not find *in-situ* preserved specimens.

Discussions

Ecology of living individuals

According to Habe and Ito (1965) and Okutani (1986), *M. kurilensis* is usually found byssally attached to rock surfaces. Okutani *et al*. (1989) reported collecting *M. kurilensis* with a dredge from a gravelly sandy bottom, but these authors also considered *M. kurilensis* to be a byssally attached, rocky-bottom dweller.

However, the shell morphology of *M. kurilensis* suggests otherwise. The shell has a moderately reduced anterior adductor, and a cylindrical shell form with an anterior lobe, showing clearly that this species is a soft-bottom endobyssate species, as demonstrated by Stanley (1970, 1972) and Seed (1980). Epibyssate species, in contrast, have a highly reduced anterior adductor inside, a triangular shell form and no anterior lobe. Stanley (1970 ; 1972) stated that *Modiolus modiolus* normally lives with between half to two thirds of its shell buried in stable gravelly sand. Specimens sampled from the gravelly bottom reported by Okutani *et al*. (1989) further confirm this observation. Judging from Stanley's observation and his functional analysis, an epifaunal life habit on rocks as observed by Habe and Ito (1965) and Okutani (1986) is probably a fortuitous example, and the normal life habit of the species must be endobyssate. The presence of encrustation on the postero-dorsal surface of shells of extant specimens of *M. kurilensis* stranded on the beach near Usu-wan, Hokkaido (senior author's personal collection) also supports this interpretation. Specimens dredged from off Wakkanai, near the northern end of Hokkaido, show similar localized encrustation, suggesting an endobyssate life habit. Stanley (1972) stated that five out of the eight species of *Modiolus* which he studied live with partial or complete burial in a soft substratum, but may also occasionally be found attached epifaunally to hard substrata because of the vagaries of larval settlement,

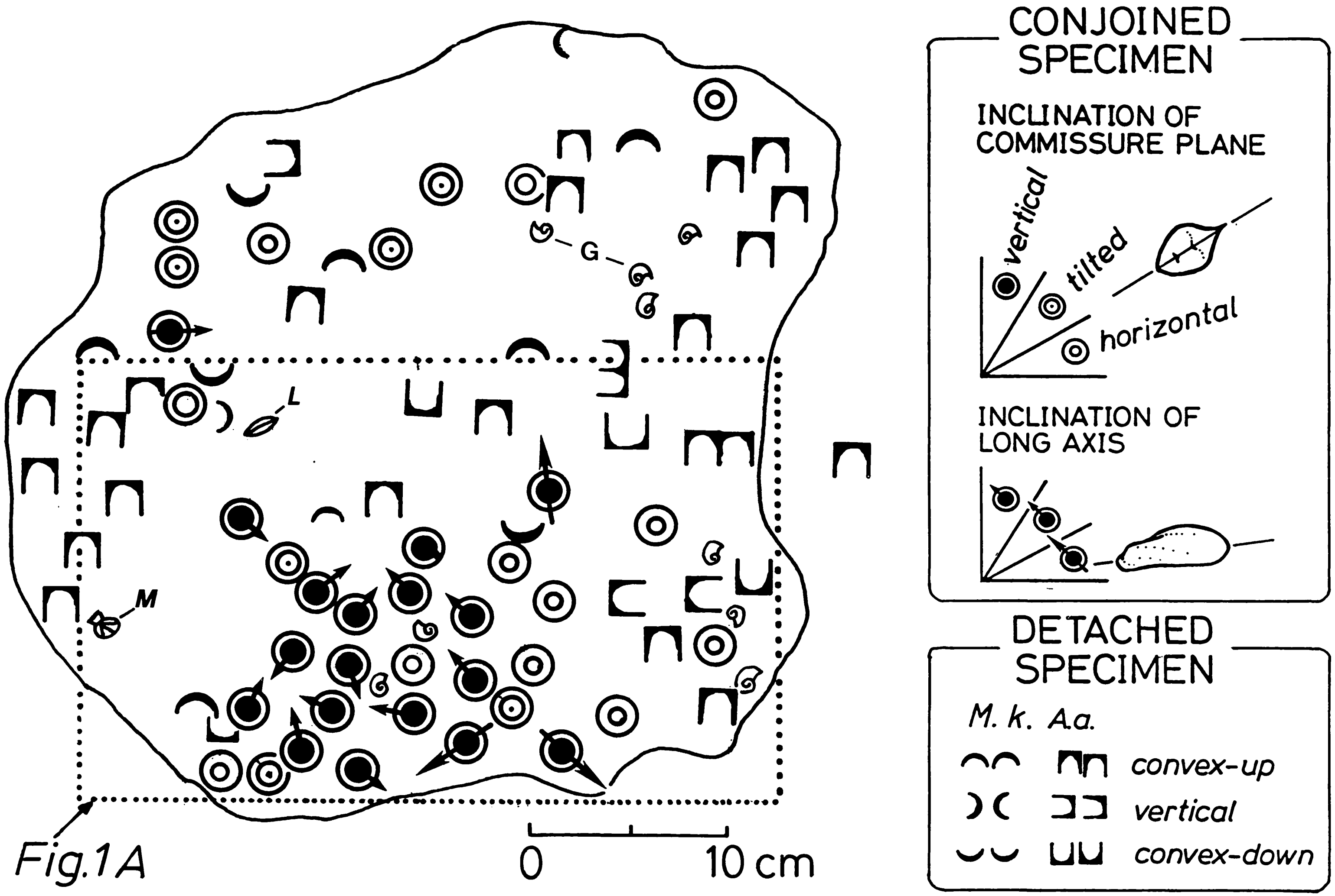

Figure 2. Spatial distribution of individuals and their mode of occurrence of *Modiolus kurilensis* and *Anadara amicula*. Inclinations of commissure plane of conjoined specimens are shown as vertical, tilted and horizontal. For vertical specimen, inclination of the long axis is shown. Distribution of detached specimens is also illustrated. Note the convex-up shell orientation is common for *Anadara amicula* specimens. M. : a juvenile specimen of *Mizuhopecten tokyoensis hokurikuensis*, L. : an *in-situ* specimen of *Lucinoma annulata*, G. : Gastropoda, *M. k.* : *Modiolus kurilensis*, *A.a.* : *Anadara amicula*

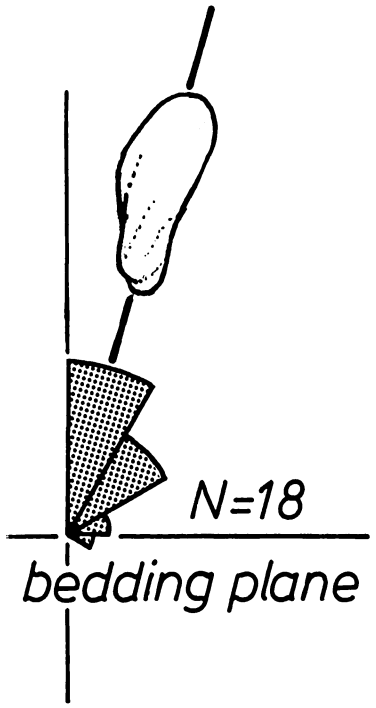

Figure 3. Preserved life orientation of *Modiolus kurilensis*.

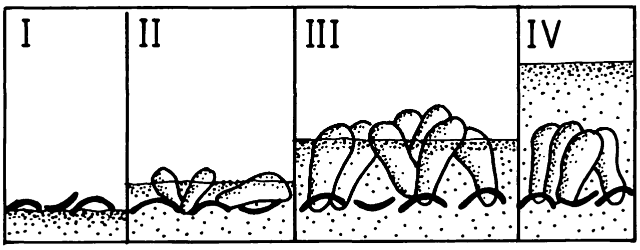

Figure 4. Schematic representation of stages of the establishment of the *Modiolus kurilensis* colony. I : shell pavement with only one layer thick shells, II : shelly substrate too shallowly covered by soft substrate to be colonized by *Modiolus*, III : shelly softground, most preferable condition for colonization by *Modiolus*, IV : shelly substrate too thickly covered by soft sediment to be colonized by *Modiolus*.

usually tending to lodge in crannies and crevices.

From the above discussion and our observation of the fossil colony, it is concluded that *M. kurilensis* is basically a soft-bottom dweller but that establishment of the colony required the initial presence of stable hard material in the substrata. The mode of life of this animal may thus be regarded as a transitional one between soft- and hard-bottom dwellers, and it is referred to as a shelly soft-bottom dweller or shell-gravel dweller.

Environmental conditions for and against colonization, and preservation of *Modiolus kurilensis*

Modiolus kurilensis is not common in the Omma Formation, according to the stratigraphic distribution chart of molluscs in the Omma Formation by Kitamura (1991b). This was also confirmed by our observation. Four different environmental factors are discussed below to explain this.

Modiolus kurilensis is a cold-water species. Climatic changes concomitant with the eustatic sedimentary cycles have therefore undoubtedly limited its distribution ; the warmer periods represented by the middle unit of each cycle probably did not allow colonization by *M. kurilensis*. It is thus expected to occur only in cycle-bounding shell beds for which the marine climate is inferred to have been reasonably cold (Kitamura and Kondo, 1990).

Also ambient energy level may have affected the distribution of *M. kurilensis*. Kitamura (1991) reconstructed that the *Anadara-Clinocardium* associations in which the *Modiolus* colony was included were deposited in a cold water regime of water depth shallower than 20-30 m in an embayment. The environmental setting of the middle unit of the Omma Formation is inferred to have been of higher energy, as shown by the generally sandier sediment texture and common occurrence of open coast species such as *Macoma sectior* and *Peronidia venulosa*. Though there is little direct information, it is likely that *M. kurilensis* prefers a sheltered environment, because of its endobyssate mode of life which needs substratum stability.

The physical condition of the substrate is considered important in the establishment of the *Modiolus* colony. Two different shelly substrata may be distinguished: shell pavement (Figure 4-I) and shelly softground (Figure 4-III). Shell pavement refers to a substratum carpeted by a layer of shells. This does provide a stable basis for many epibionts, but it is not suited for moderately large endobyssate bivalves like *M. kurilensis*. A shelly softground includes sufficient shell material within the soft substratum to allow colonization by *M. kurilensis*. We need, therefore, to distinguish these two different substratum conditions.

In relation to the above discussion, the mechanism of deposition of different shell beds may have determined the physical characteristics of the substrate and thus explain the relatively uncommon occurrence of *M. kurilensis* is the cycle-bounding shell beds of the middle Omma Formation.

Kitamura and Kondo (1990) demonstrated that the shell beds bounding sedimentary cycles in the Omma Formation were formed during low stands of sea level during 41 thousand-year glacio-eustatic cycles of the early Pleistocene. Formation of the shell beds is, therefore, the result of relatively long periods of deposition. However, Kondo and Kitamura (1988) have pointed out that the shell beds are often dominated by infauna, which only rarely show weathering or damage due to *Cliona* boring or encrustation by calcareous algae, barnacles or bryozoan. They therefore concluded that the formation of shell beds involved rapid burial events. These observations are however not consistent with the general model for shell accumulation resulting from low rates of sedimentation. Perhaps the cycle-bounding shell beds were formed by repetitious storm deposition, and long-term environmental changes during lowstand of sea-level were thereby still recorded.

Accumulated shells were buried in well sorted very fine sand immediately after the emplacement event. Reworked shells were buried too deeply to be used as a basis to attach to with a byssus. Consequently, a shelly soft bottom condition was not available for *Modiolus* during formation of the shell beds. In contrast, the shell lenses of *Anadara* in the lower unit of the Omma Formation are not associated with a rapid burial event and colonization was possible.

Kidwell and Jablonski (1983) recognized two types of shell concentration associated with low net sedimentation; (i) undisturbed reduced sedimentation, which permits nearly continuous maintenance of a shelly substratum (low total sedimentation), and (ii) repeated physical disturbance, producing a shell concentration containing both epifaunal and infaunal taxa (high total sedimentation). The basal shell bed in the middle unit of the Omma Formation is understood as a further extreme type of higher total sedimentation, in which almost no shelly substratum appeared on the surface during formation of the shell bed (highest total sedimentation).

In summary, it is concluded that a shelly softground which could be colonized by endobyssate bivalve was only rarely available on the inner shelf muddy sand bottom during deposition of the Omma Formation.

Lastly preservation is considered to be important in producing the observed pattern of stratigraphic distribution of *Modiolus* shell and colonies. Even if a *Modiolus* colony was successfully established during deposition of a cycle-bounding shell bed, it is unlikely to have been preserved *in situ*, because bottom sediment reworking to a depth of 10-20 cm constantly occurred. In fact, reworking may have reached 50 cm depth, as inferred from the analysis of preservation of bivalve life positions. The relatively uncommon scattered shells of *M. kurilensis* which occur in the Omma Formation may represent reworked and transported shells during such high energy events.

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Fossil Mollusca of the Lower Miocene Yotsuyaku Formation in the Ninohe district, Iwate Prefecture, Northeast Japan

Part 1. General consideration of the fauna

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Abstract. The fossil Mollusca of the Lower Miocene Yotsuyaku Formation in Iwate Prefecture were studied and 20 species of Bivalvia, 15 species of Gastropoda and 1 species of Scaphopoda were discriminated. They are divided into Type I and II assemblages from a paleoecological viewpoint ; Type I is composed of brackish to shallow embaymental elements ; Type II indicates middle to lower sublittoral muddy bottom environments. The assemblage generally changes from Type I to II in ascending order. *Dosinia* (*Phacosoma*) *kawagensis* Araki, *Ruditapes miyamurensis* (Itoigawa), *Trapezium* (*Neotrapezium*) *modiolaeforme* Oyama and Saka, *Tateiwaia* sp. nov. and *Vicaryella "bacula"* (Yokoyama) are reported for the first time in the formation. These species seldom occur in Northeast Japan although they have often been reported from the lower part of the First Setouchi Miocene Series. Comparison of Type I with brackish to intertidal elements of the Kadonosawa Fauna of Northeast Japan reveals that characteristic elements of the "Arcid-Potamid fauna" such as *Anadara* (*Hataiarca*) spp. are not found in the formation, and several genera are represented by different species. The Kadonosawa Fauna of Southwest Japan has been divided into the Akeyo and Kurosedani Faunas in ascending order. Similar stratigraphic differences in the shallow warm water marine molluscan fauna from upper Lower to lower Middle Miocene sequences have also been recognized in several districts in Northeast Japan. These facts support the conclusion that the molluscan fauna of the Yotsuyaku Formation corresponds to the Akeyo Fauna of Southwest Japan, and the Kadonosawa Fauna in Northeast Japan is also divided into lower and upper portions.

Key words : Yotsuyaku Formation, Lower Miocene, Northeast Japan, Akeyo and Kadonosawa Faunas

Introduction

Tertiary sequences which yield a lot of molluscs are widely and thickly distributed in the northwestern margin of the Kitakami Mountains, and many geological and paleontological studies have been carried out (e.g., Otuka, 1934 ; Hatai, 1936, 1940 ; Hayakawa *et al*., 1954 ; Chinzei, 1958a, b, 1966 ; Aoki, 1960 ; Chinzei and Iwasaki, 1967 ; Samata, 1976 ; Maruyama, 1984 ; Irizuki and Matsubara, 1994). As a result, it is well known that the Lower Miocene sequences have a warm water shallow marine molluscan fauna, whereas the Middle Miocene sequences yield a colder fauna. The former is well known as the Kadonosawa Fauna (Otuka, 1939, 1941 ; Chinzei, 1963) which represents tropical to subtropical environments around the Japanese Islands, except for northern Hokkaido, around 19.0- or 16.5-15.0 Ma in age (Chinzei, 1978, 1981a, b, 1983, 1986a, b ; Tsuchi, *ed*., 1981 ; Tsuchi and IGCP-114 National Working Group, 1984 ; Itoigawa, 1987, 1988 ; Ogasawara, 1988).

The Yotsuyaku Formation is the oldest Neogene in the district and previous investigators have reported marine molluscan fossils from its lower part. The molluscan fossils from the formation were first reported by Yabe (1921) making reference to the Tertiary geology of Shimizu (1919 MS) (Figure 3). He noted the occurrence of molluscs in Shimizu's "Black Soft Shale" of the Yotsuyaku Group. Subsequently, Otuka (1934), who studied the geology and paleontology of the district, introduced the "Koiwai Shell Beds" for the horizon yielding molluscs in his Yotsuyaku Series. Thereafter, Hayakawa *et al*. (1954) and Chinzei (1958a, b) listed some molluscan fossils from the formation, but they were neither illustrated nor described. Chinzei (1963, 1979) included these molluscs in addition to those from the overlying Tate Conglomeratic Sandstone Member of the Kadonosawa Formation as the type Kadonosawa Fauna.

Although the occurrence of molluscan fossils in this formation is known, the constituents of the fauna are not fully understood. During the present study, it became clear that the components of the Yotsuyaku Formation are different from those of the "Kadonosawa Fauna". The aim of the present study is to describe the molluscan fauna of the Yotsuyaku Formation and determine the stratigraphic differences from the Kadonosawa Fauna of Northeast Japan.

Geological setting and age

Tertiary sequences of the Ninohe and Sannohe districts are divided into two groups, namely, the Shiratorigawa and Sannohe Groups in ascending order (Chinzei, 1958a, b). These sequences unconformably overlie pre-Tertiary basement rocks that are distributed on a NW-SE axis in the eastern and western parts of the study area, and broadly, they form a gentle synclinal structure plunging NW (Figure 1). The Yotsuyaku Formation (Hayakawa *et al.*, 1954) is the oldest Neogene sequence in the district (Figure 2), unconformably overlying or in fault contact with the pre-Tertiary basement rocks which are composed of chert, schist and limestone along with plutonic rocks such as gabbro and granodiorite. In general, this formation is covered by the Kadonosawa Formation conformably. The Yotsuyaku Formation consists mainly of irregular alternating beds of mudstone, sandstone and conglomerate with intercalated pyroclastic rocks in its lower and middle portions. The formation is divided into five members in ascending order: Matsukura Mudstone, Sandstone and Conglomerate, Nisatai Dacite, Koiwai Mudstone, Sandstone and Conglomerate, Keiseitôge Andesite, and Sugohata Mudstone, Sandstone and Conglomerate Members. Among them, only the Koiwai Mudstone, Sandstone and Conglomerate Member is of marine origin, containing molluscan fossils, while the other members are non-marine, yielding erect stumps and plant leaves; the Nisatai Dacite Member contains no fossils. The thickness of the formation is about 380 m in the upper course of the Shiratori River. It increases toward the south and east where the pre-Tertiary basement is distributed. The Sugohata Mudstone, Sandstone and Conglomerate Member unconformably covers the basement and the Nisatai Dacite Member, without the Keiseitôge Andesite and lower members being present, in the northern and western areas.

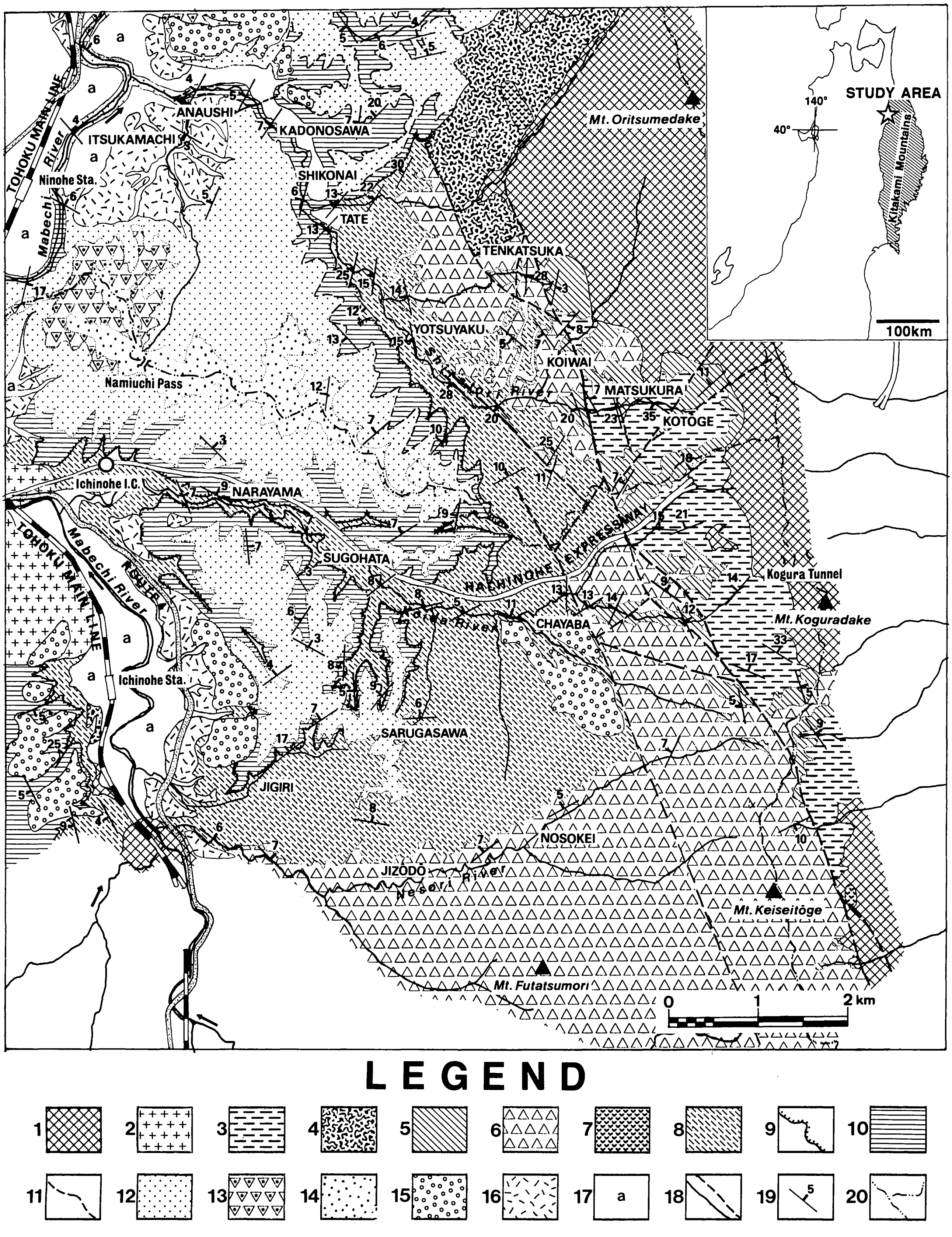
The Matsukura Mudstone, Sandstone and Conglomerate Member here proposed is the lowermost unit of the Yotsuyaku Formation and consists of non-marine clastic deposits. It corresponds to the "Lower Plant Beds" of Otuka (1934) or the lower half of the "Koiwai Mudstone, Sandstone and Conglomerate Member" of Chinzei (1958a). The member consists of alternating beds of light gray mudstone, tuffaceous sandstone and pebble to cobble conglomerate sometimes with intercalated thin lignite beds. The type locality of this member is a riverside exposure on the Shiratori River south of Matsukura, Ninohe City. The thickness of the member is about 80 m in the type locality.

The Nisatai Dacite Member here defined consists of dacitic lava, massive welded tuff and light gray pumice tuff, rich in biotite. This member is mainly distributed in the northern part of the study area apart from the other members, and therefore the stratigraphic position of this dacitic mass has been controversial (Otuka, 1934; Hayakawa *et al.*, 1954; Chinzei, 1958a, 1966; Samata, 1976) (Figure 3). However, the present writer could find that the "Nisatai Dacite" overlies the Matsukura Member (column A in Figure 4), while the basal part of the Koiwai Mudstone, Sandstone and Conglomerate Member includes cobble to boulder derived from the dacite (column C in Figure 4). Consequently, the "Nisatai Dacite" is intercalated in the lower part of the Yotsuyaku Formation as shown in Figure 2.

The Koiwai Mudstone, Sandstone and Conglomerate Member, here redefined, corresponds to the "Koiwai Shell Beds" of Otuka (1934), or the upper half of the Koiwai Mudstone, Sandstone and Conglomerate Member of Chinzei (1958a). The name of the member was originally used for clastic facies overlain by the Keiseitôge Andesite Member (Chinzei, 1958a), but it is here used for marine deposits in the lower part of the formation. The member is composed of dark gray mudstone and bluish gray sandstone with conglomerate in the basal part consisting of subrounded to rounded pebbles to cobbles of basement rocks and dacitic rocks derived from the Nisatai Dacite Member. The thickness of the member is about 120 m at the type locality on the bank of the Shiratori River, about 500 m south of Koiwai, Nihohe City. Molluscan fossils do not occur in the basal conglomerate, but they are frequently found in mudstone and sandstone, where there are shell beds.

The Keiseitôge Andesite Member (Hayakawa *et al.*, 1954) conformably overlying the Koiwai Mudstone, Sand-

Figure 1. Geological map of the study area. Legend; 1-2. Pre-Tertiary Basement Rocks (1. sedimentary and metamorphic rocks; 2. plutonic rocks); 3-8. Yotsuyaku Formation. (3. Matsukura Mudstone, Sandstone and Conglomerate Member; 4. Nisatai Dacite Member; 5. Koiwai Mudstone, Sandstone and Conglomerate Member; 6-7. Keiseitôge Andesite Member (6. pyroclastic rocks; 7. intrusive rocks); 8. Sugohata Mudstone, Sandstone and Conglomerate Member), 9-10. Kadonosawa Formation (9. Tate Conglomeratic Sandstone Member; 10. Shikonai Siltstone Member); 11-14. Suenomatsuyama Formation (11. Anaushi Conglomeratic Sandstone Member; 12. Itsukamachi Sandstone Member; 13. Aikawa Andesite Member; 14. Maisawa Sandstone Member); 15-17. Quaternary deposits (15. terrace deposit; 16. Towada Volcano ejecta; 17. alluvial deposit); 18. Fault (full line=observed, dashed line=inferred); 19. dip and strike; 20. boundary of county.


STUDY AREA
140°
40°
Kitakami Mountains
100km
Mt. Oritsumedake
TOHOKU MAIN LINE
Mabechi River
Ninohe Sta.
ITSUKAMACHI
ANAUSHI
KADONOSAWA
SHIKONAI
TATE
TENKATSUKA
YOTSUYAKU
KOIWAI
MATSUKURA
KOTOGE
Namiuchi Pass
Ichinohe I.C.
NARAYAMA
SUGOHATA
HACHINOHE EXPRESSWAY
Kogura Tunnel
Mt. Koguradake
CHAYABA
Route 4
Ichinohe Sta.
SARUGASAWA
JIGIRI
NOSOKEI
JIZODO
Mt. Keiseitōge
Mt. Futatsumori
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LEGEND
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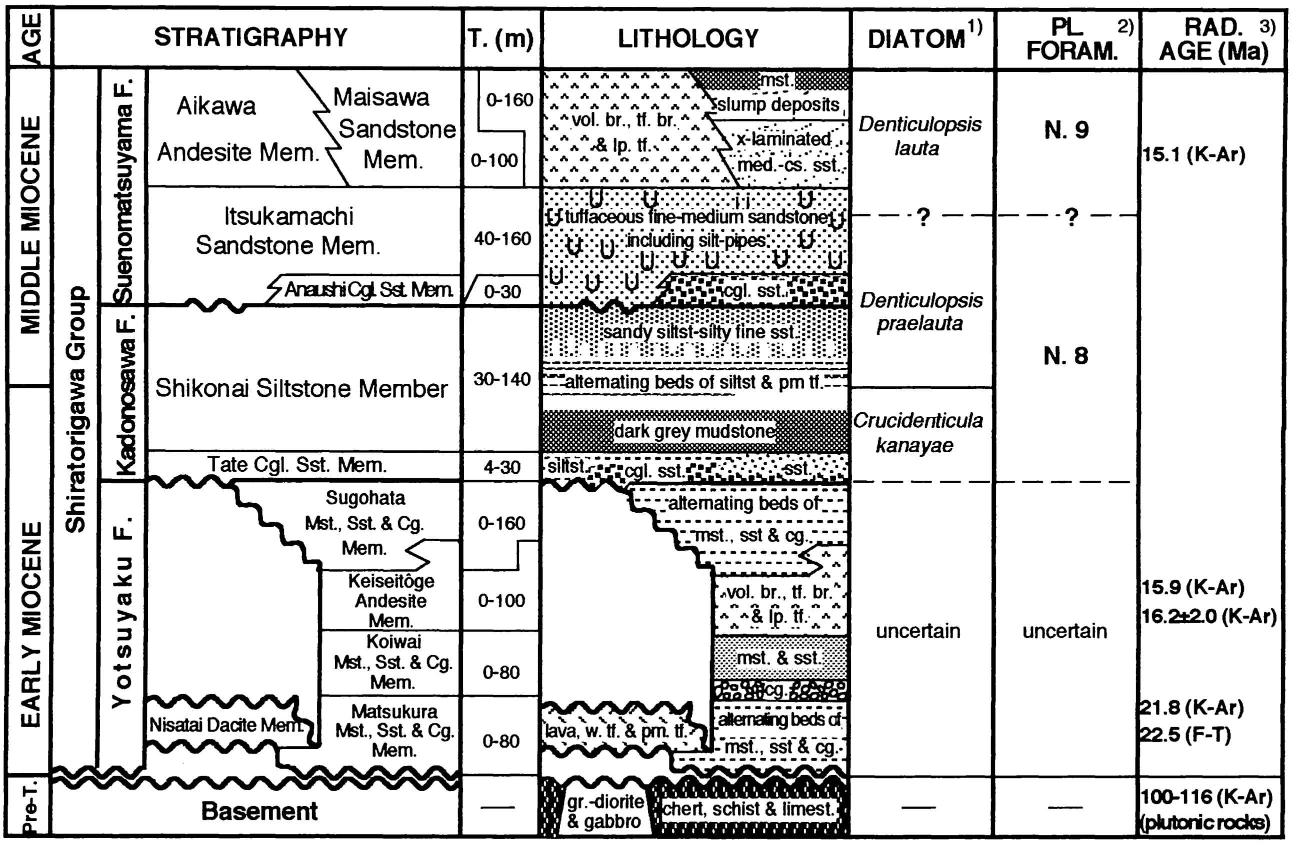

Figure 2. Stratigraphy of the Shiratorigawa Group in the eastern part of the Ninohe district, Iwate Prefecture. Biostratigraphic and radiometric data are based on the following studies ; 1)diatom : Akiba (1977), Koizumi (1979), Oda *et al.* (1983, 1984), Maruyama (1984), Irizuki and Matsubara (1994) ; 2)planktonic foraminifera : Samata (1976), Oda *et al.* (1983, 1984), Irizuki and Matsubara (1994) ; 3)radiometric age : Kawano and Ueda (1965), Kimura (1986, 1988), Kubo (1987).

stone and Conglomerate Member consists of andesitic pyroclastic rocks. The lithofacies changes laterally into volcanic breccia to water-worn tuff breccia and lapilli tuff and decreases in thickness towards the north of the study area. Therefore, it is considered that the eruptive vent for the andesite existed in the southeast of the study area.

The Sugohata Mudstone, Sandstone and Conglomerate Member (Chinzei, 1958a) occupies the upper part of the formation. It is composed of irregular alternating beds of lignitic mudstone, tuffaceous mudstone and sandstone, and pebble to cobble conglomerate, consisting of andesite gravels derived from the Keiseitôge Andesite Member. The conglomerate beds increase in frequency and thickness towards the south, whereas in the vicinity of the Shiratori River they are rarely found. Maximum thickness of the member is about 150 m.

The geological age of the Yotsuyaku Formation is still unclear from a biostatigraphic point of view, although some radiometric ages have been reported. Kimura (1986, 1988) reported K-Ar and fission track ages of the Nisatai Dacite and Keiseitôge Andesite Members are 21.8 and 22.5 Ma for the former, and 15.9 Ma for the latter. In addition, Kubo (1987) studied the K-Ar age of an andesitic "tuff breccia" correlated to the Keiseitôge Andesite Member, and obtained a dating of 16.2±2.0 Ma. Further, the Kadonosawa Formation, covering the formation conformably, is referred to the *Crucidenticula kanayae* and *Denticulopsis praelauta* Zones of Akiba (1986) (Akiba, 1977 ; Koizumi, 1979, 1986b ; Maruyama, 1984 ; Irizuki and Matsubara, 1994). Judging from these data, the Koiwai Mudstone, Sandstone and Conglomerate Member with its contained Mollusca is considered to be upper Lower Miocene. In this study, although diatom fossils are for the first time obtained from the member, the diatom zone has not been determined because of the lack of index species, poor preservation and lesser frequency

Figure 3. Stratigraphic comparison between the present and previous studies. Two hatched lines in Yabe (1921), Otuka (1934) and Hayakawa *et al.* (1954) indicate formation boundary between the Kadonosawa and Suenomatsuyama Formations and the upper limit of the Suenomatsuyama Formation of the present study.

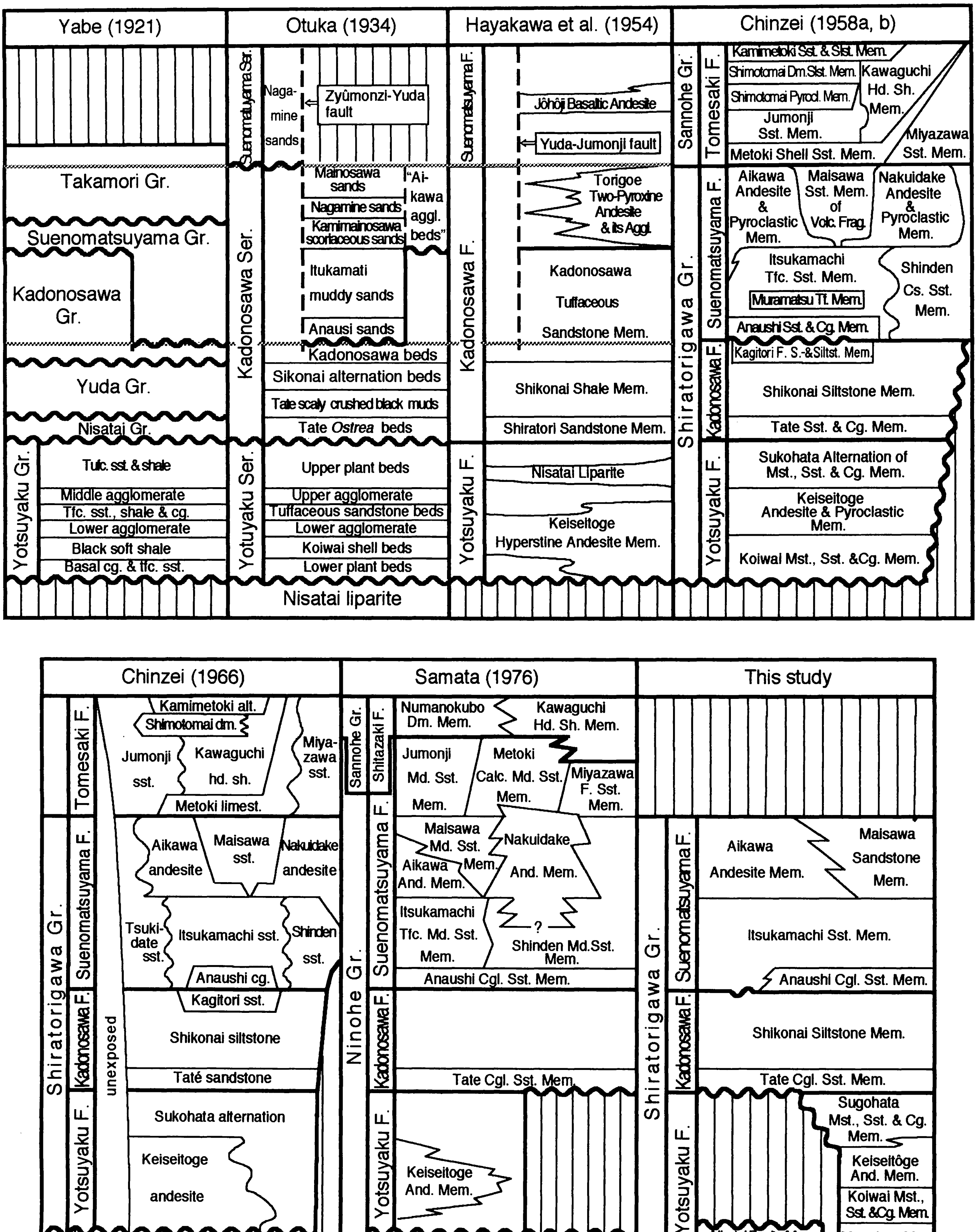
Yabe (1921)
Otuka (1934)
Hayakawa et al. (1954)
Chinzei (1958a, b)
Takamori Gr.
Suenomatsuyama Gr.
Kadonosawa Gr.
Yuda Gr.
Nisatai Gr.
Yotsuyaku Gr.
Tufc. sst. & shale
Middle agglomerate
Tfc. sst., shale & cg.
Lower agglomerate
Black soft shale
Basal cg. & tfc. sst.
Suenomatsuyama Ser.
Kadonosawa Ser.
Yotuyaku Ser.
Naga-mine sands
Zyûmonzi-Yuda fault
Mainosawa sands
Nagamine sands
Kamimainosawa scoriaceous sands
"Ai-kawa aggl. beds"
Itukamati muddy sands
Anausi sands
Kadonosawa beds
Sikonai alternation beds
Tate scaly crushed black muds
Tate Ostrea beds
Upper plant beds
Upper agglomerate
Tuffaceous sandstone beds
Lower agglomerate
Koiwai shell beds
Lower plant beds
Nisatai liparite
Suenomatsuyama F.
Kadonosawa F.
Yotsuyaku F.
Jôhôji Basaltic Andesite
Yuda-Jumonji fault
Torigoe Two-Pyroxine Andesite & its Aggl.
Kadonosawa Tuffaceous Sandstone Mem.
Shikonai Shale Mem.
Shiratori Sandstone Mem.
Nisatai Liparite
Keiseitoge Hyperstine Andesite Mem.
Sannohe Gr.
Tomesaki F.
Shiratorigawa Gr.
Suenomatsuyama F.
Kadonosawa F.
Yotsuyaku F.
Kamimetoki Sst. & Slst. Mem.
Shimotomai Dm. Slst. Mem.
Shimotomai Pyrocl. Mem.
Kawaguchi Hd. Sh. Mem.
Jumonji Sst. Mem.
Miyazawa Sst. Mem.
Metoki Shell Sst. Mem.
Aikawa Andesite & Pyroclastic Mem.
Maisawa Sst. Mem. of Volc. Frag.
Nakuidake Andesite & Pyroclastic Mem.
Itsukamachi Tfc. Sst. Mem.
Muramatsu Tf. Mem.
Shinden Cs. Sst. Mem.
Anaushi Sst. & Cg. Mem.
Kagitori F. S.-& Siltst. Mem.
Shikonai Siltstone Mem.
Tate Sst. & Cg. Mem.
Sukohata Alternation of Mst., Sst. & Cg. Mem.
Keiseitoge Andesite & Pyroclastic Mem.
Koiwai Mst., Sst. & Cg. Mem.
Chinzei (1966)
Samata (1976)
This study
Shiratorigawa Gr.
Tomesaki F.
Suenomatsuyama F.
Kadonosawa F.
Yotsuyaku F.
unexposed
Kamimetoki alt.
Shimotomai dm.
Jumonji sst.
Kawaguchi hd. sh.
Miya-zawa sst.
Metoki limest.
Aikawa andesite
Maisawa sst.
Nakuidake andesite
Tsuki-date sst.
Itsukamachi sst.
Shinden sst.
Anaushi cg.
Kagitori sst.
Shikonai siltstone
Taté sandstone
Sukohata alternation
Keiseitoge andesite
Sannohe Gr.
Shitazaki F.
Ninohe Gr.
Suenomatsuyama F.
Kadonosawa F.
Yotsuyaku F.
Numanokubo Dm. Mem.
Kawaguchi Hd. Sh. Mem.
Jumonji Md. Sst. Mem.
Metoki Calc. Md. Sst. Mem.
Miyazawa F. Sst. Mem.
Maisawa Md. Sst. Mem.
Aikawa And. Mem.
Nakuidake And. Mem.
Itsukamachi Tfc. Md. Sst. Mem.
?
Shinden Md. Sst. Mem.
Anaushi Cgl. Sst. Mem.
Tate Cgl. Sst. Mem.
Keiseitoge And. Mem.
Nisatai F.
Shiratorigawa Gr.
Suenomatsuyama F.
Kadonosawa F.
Yotsuyaku F.
Aikawa Andesite Mem.
Maisawa Sandstone Mem.
Itsukamachi Sst. Mem.
Anaushi Cgl. Sst. Mem.
Shikonai Siltstone Mem.
Tate Cgl. Sst. Mem.
Sugohata Mst., Sst. & Cg. Mem.
Keiseitôge And. Mem.
Koiwai Mst., Sst. & Cg. Mem.
Nisatai Dacite Mem.
Matsukura Mst., Sst. & Cg. Mem.

Figure 3.

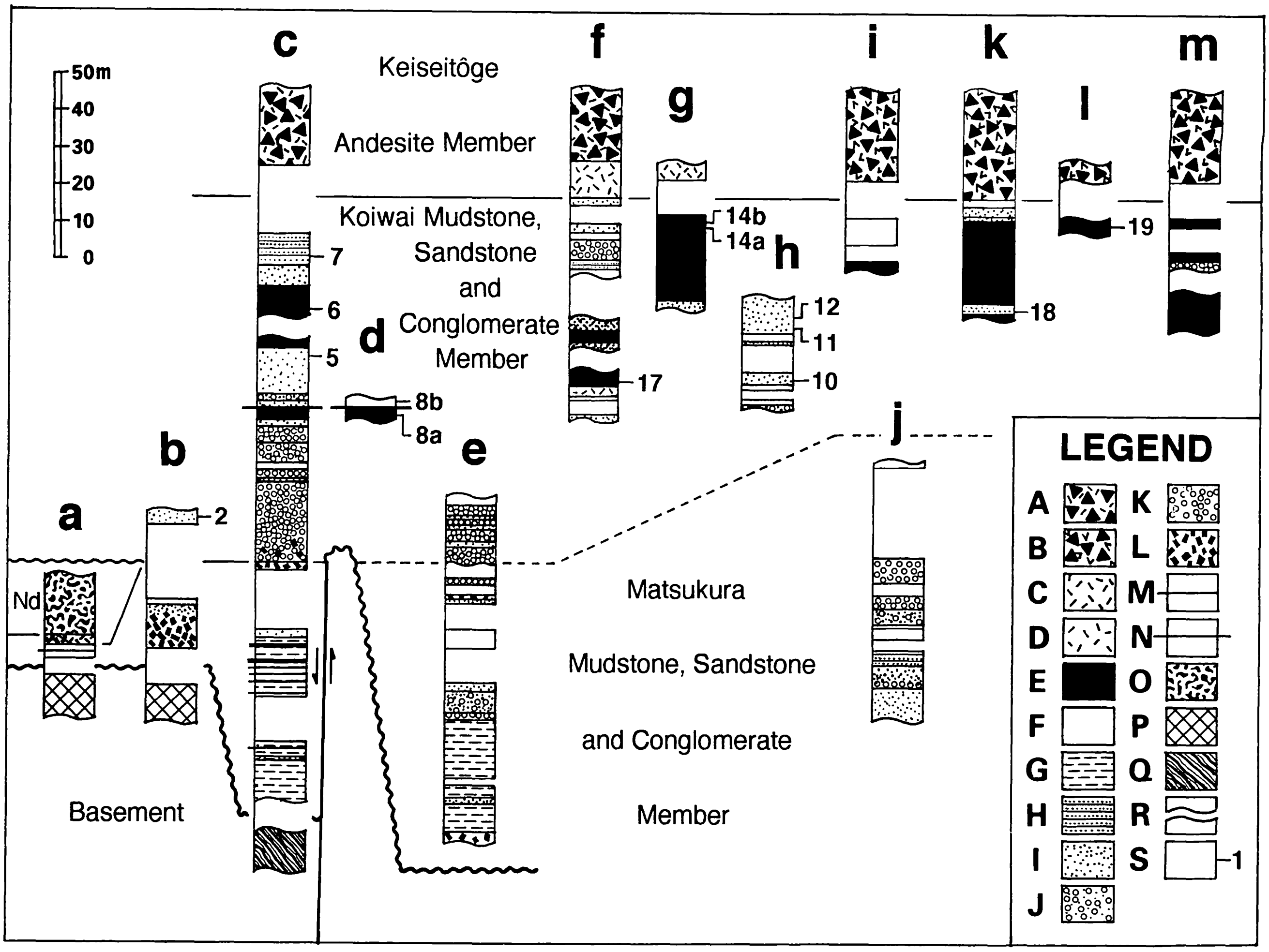

Figure 4. Columnar sections for the selected sites in the lower part of the Yotsuyaku Formation (a to m in Figure 5). Legend: A. tuff braccia; B. volcanic breccia; C. pumice tuff; D. fine tuff; E. dark gray mudstone; F. siltstone; G. alternating beds of mudstone and sandstone (mudstone dominant); H. alternating beds of mudstone and sandstone (sandstone dominant); I. sandstone; J. conglomeratic sandstone; K. conglomerate; L. talus breccia; M. lignite bed; N. key tuff bed; O. dacite; P. chert; Q. schist; R. fault; S. fossil horizon.

(Table 1).

Molluscan assemblages and paleoenvironment

Twenty species of Bivalvia belonging to 19 genera, 15 species of Gastropoda belonging to 12 genera, and one species of Scaphopoda have been identified from 21 localities in the Koiwai Mudstone, Sandstone and Conglomerate Member of the Yotsuyaku Formation (Figure 5, Table 2). Among them, one species of Bivalvia and two of Gastropoda are new to science. These molluscs are to be described in Part 2.

a. Molluscan assemblages

Two types of molluscan assemblage groups are recognized based on co-occurrences and frequency of the characteristic species. The first is subdivided into seven and the other into two assemblages (Figure 6). Of the localities, 1, 3 and 16 must be excluded from consideration because at these localities the molluscs show an allochthonous mode of occurrence.

Type I: Type I is characterized by the following species: *Nipponomarcia nakamurai* (Ikebe), *Raditapes miyamurensis* (Itoigawa), *Hiatula minoensis* (Yokoyama), *Vicaryella otukai* (Nomura), *Tateiwaia* sp. nov. and *Crassostrea gigas* (Thunberg).

Ia. *Nipponomarcia* Assemblage: The *Nipponomarcia* Assemblage is characterized by the greatly predominant occurrence of *Nipponomarcia nakamurai* (Ikebe). Associated species are much less common. This assemblage is often recognized in dark gray mudstone forming shell beds with thickness of 30 cm to 1 m. It is considered to be the same as the *Nipponomarcia* Assemblage of Shibata (1978).

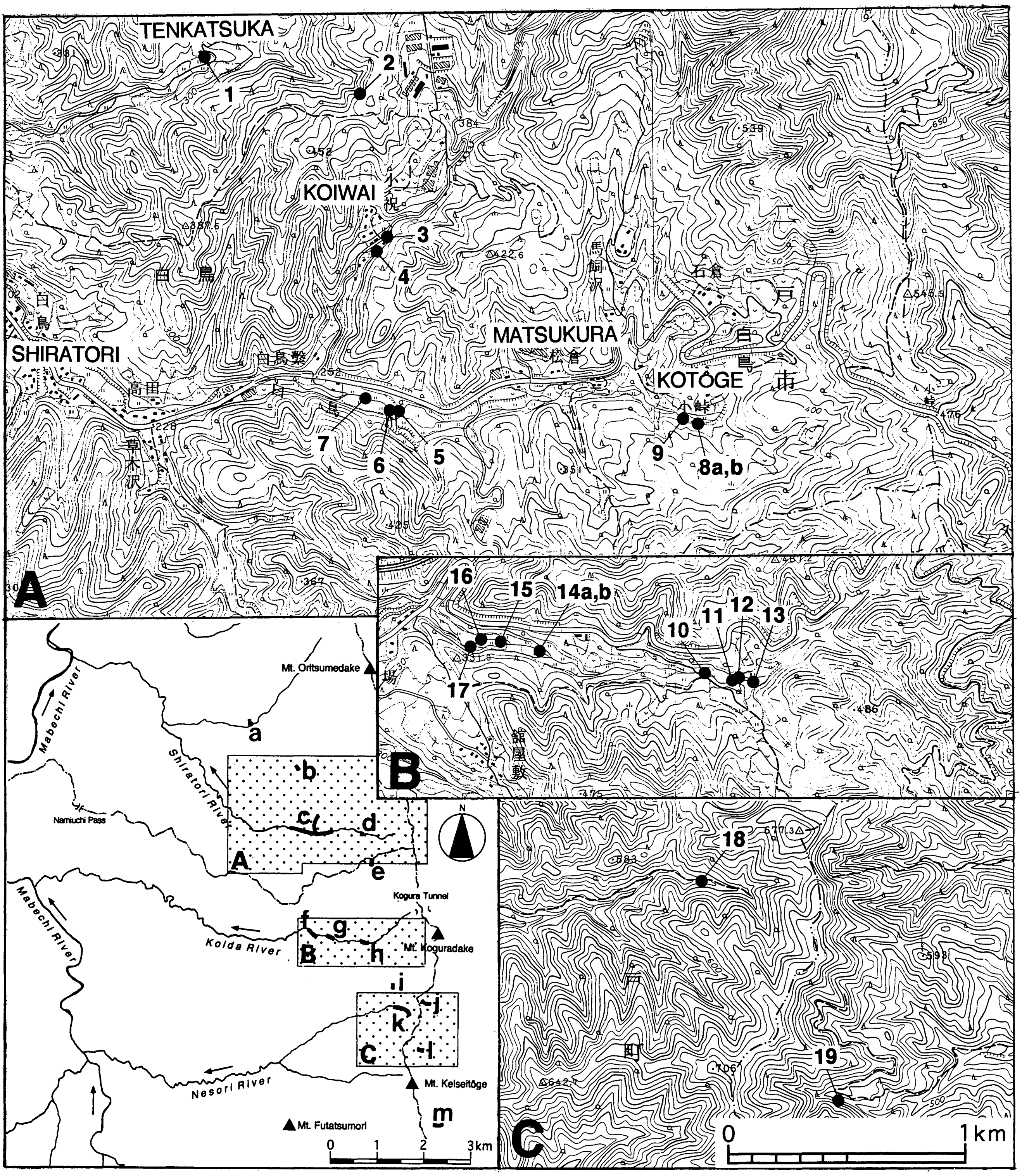

Figure 5. Locality map of molluscan collections from the Yotsuyaku Formation. (Base map adopted from Quadrangle "Ichinohe" and "Ibonai", 1 : 25,000-scale topographic map of Japan, Geographical Survey Institute). Lower left figure indicates the study area illustrated in Figure 1 with dotted areas (A to C) that are enlarged on the upper (A), middle right (B) and lower right (C) figures, and showing columnar section lines (a to m).

Table 1. Diatoms from the Koiwai Mudstone, Sandstone and Conglomerate Member of The Yotsuyaku Formation (identified by Dr. Yanagisawa). Sample number is the same as locality number of molluscs. + = occurrence.

Species name / Sample number	14a	19
Arachnoidiscus spp.	+	+
Aulacoseira spp.	+	
Coscinodiscus spp. (fragments)	+	+
Diploneis sp.		+
Grammatophora spp.		+
Hyalodiscus obsoletus Sheshukova-Porezkaya	+	
Ikebea tenuis (Brun) Akiba	+	
Paralia sulcata (Ehrenberg) Cleve	+	+
Stephanopyxis spp. (fragments)	+	+
Thalassionema nitzschioides (Grunow) H. et M. Peragallo	+	+
Resting spore of *Chaetoceros*	+	+

Ib. *Hiatula* Assemblage: The *Hiatula* Assemblage is recognized by the common occurrence of *Hiatula minoensis* (Yokoyama) associated with *Nipponomarcia nakamurai* (Ikebe), *Ruditapes miyamurensis* (Itoigawa) and *Trapezium* (*Neotrapezium*) *modiolaeforme* (Oyama and Saka) occurring in muddy sandstone.

Ic. *Tateiwaia* Assemblage: This is the most characteristic assemblage in Type I. It is found in gray tuffaceous muddy sandstone and characterized by the common occurrence of *Tateiwaia* sp. nov. in association with *Nipponomarcia nakamurai* (Ikebe) and *Ruditapes miyamurensis* (Itoigawa). Difference from the *Hiatula* Assemblage is indicated by the frequent occurrence of *Tateiwaia* sp. nov. and the higher species diversity.

Id. *Dosinia*-*Cyclina*-*Vicaryella* Assemblage: This assemblage is characterized by the abundant occurrence of *Dosinia* (*Phacosoma*) *kawagensis* Araki, *Cyclina japonica* Kamada and *Vicaryella "bacula"* (Yokoyama) in association with *Meretrix arugai* Otuka, *Hiatula minoensis* (Yokoyama) and others. It comes from tuffaceous muddy fine to medium-grained sandstone forming shell beds. In the shell bed, many bivalves are conjoined, their commissure lines are arranged parallel to bedding and they are less water-worn. These features suggest that the assemblage was transported, even though the original composition is preserved. This assemblage corresponds

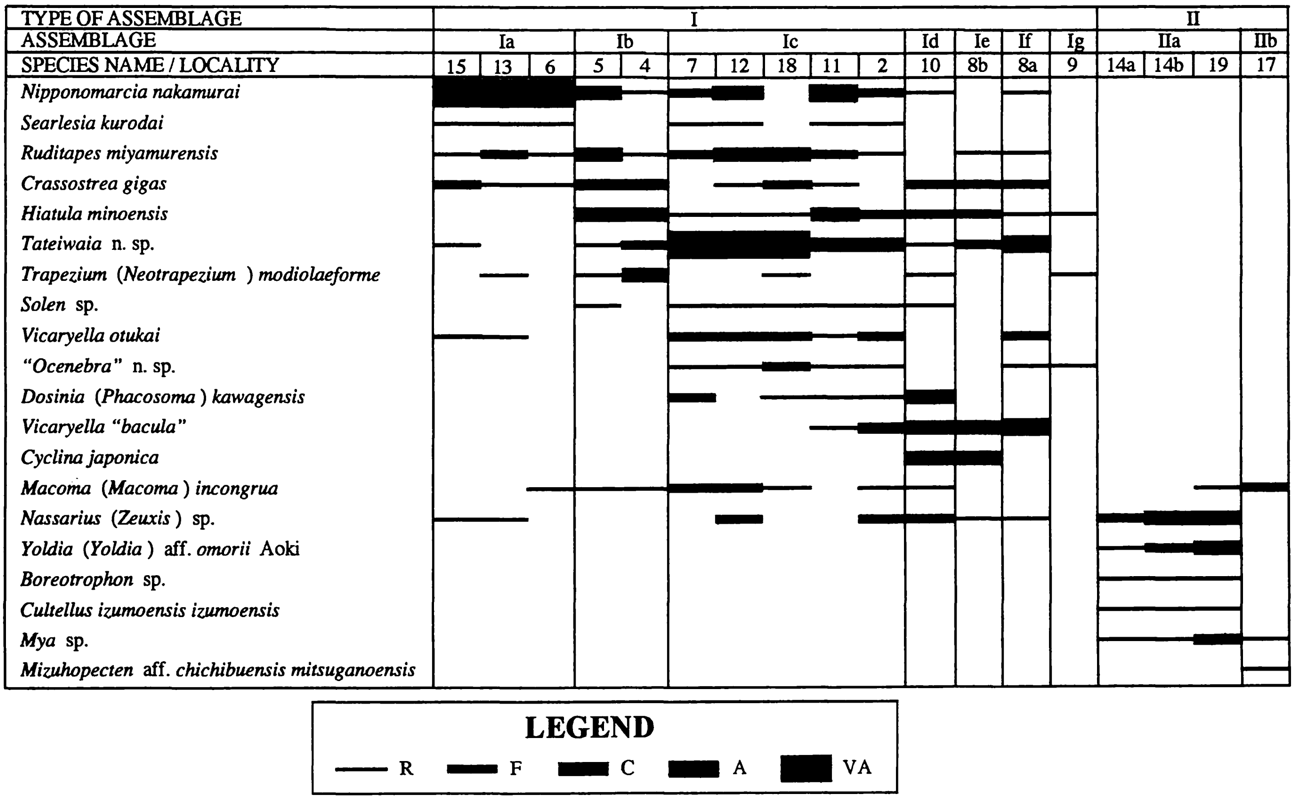

Figure 6. Molluscan assemblage of the Matsukura Mudstone, Sandstone and Conglomerate Member of the Yotsuyaku Formation. See text for explanation of the assemblages (Ia to g and IIa to b). Abundance data as for Table 2.

Table 2. Molluscan fossils from the Koiwai Mudstone, Sandstone and Conglomerate Member of the Yotsuyaku Formation. Abundance data: R=rare (1-3 specimens); F=few (4-9); C=common (10-19); A=abundant (20-29); VA=very abundant (>29). *: these new species are to be proposed in Part 2.

Species name / Locality	1	2	3	4	5	6	7	8a	8b	9	10	11	12	13	14a	14b	15	16	17	18	19
BIVALVIA																					
Yoldia (*Yoldia*) aff. *omorii* Aoki															F	F					C
Mizuhopecten aff. *chichibuensis mitsuganoensis* (Shibata)																			R		
Anomia chinensis Philippi					R			C	R					F							
Crassostrea gigas (Thunberg)	F		F	F	F	R	R	F	F		F	R	R	R			F			F	
Lucinoma cf. *acutilineata* (Conrad)															R	R		R			
Pillucina (*Wallucina*) cf. *striata* (Tokunaga)		F					R														
Felaniella ferruginata (Makiyama)																	R				
Clinocardium sp.	R	R													R	C					F
Macoma (*Macoma*) *incongrua* (v. Martens)	R	R	R	R	R	R	F	R			R		F						F	R	C
Hiatula minoensis (Yokoyama)		F		C	C		R	R	F	R	F	C	R							R	
Solen sp.		R			R		R				R	R	R							F	
Cultellus izumoensis izumoensis Yokoyama															R	R					R
Trapezium (*Neotrapezium*) n. sp.*				R							R									F	
Trapezium (*Neotrapezium*) *modiolaeforme* Oyama and Saka				C	R					R				R						R	
Dosinia (*Phacosoma*) *kawagensis* Araki		R					F			R	C	R								R	
Ruditapes miyamurensis (Itoigawa)	R	R	R	R	C	R	F	R	R			F	C	F			R			C	
Nipponomarcia nakamurai (Ikebe)	A	F	F	R	C	VA	F	R			R	A	C	VA			VA	R			
Meretrix arugai Otuka											F										
Cyclina japonica Kamada									C		C										
Mya sp.															F	R			R		F
GASTROPODA																					
Homalopoma aff. *ena* (Itoigawa)	R																				
Canthalidus sp.	R				R		R						R							R	
Littorina sp.							R						R								
Crepidula jimboana Yokoyama	R		A	R														A		F	
Tateiwaia n. sp.*		C		F	R		VA	A	F			C	VA					R		VA	
Cerithideopsilla aff. *minoensis* (Itoigawa)									R	F		R		R						R	
Vicaryella "*bacula*" (Yokoyama)		F						A	C		C	R									
Vicaryella otukai (Nomura)		F	R					F				R	F	R			R			F	
Vicaryella sp.		R																			
"*Ocenebra*" n. sp.*		R					R	R				R	R							F	
Phos (*Phos*) *notoensis* Masuda											R	R	R	F							R
Searlesia kuridai		R				R	R				R	R	R	R			R				
Nassarius (*Zeuxis*) sp.	R	F	R					R	R		F		R	R	F	C	R	C		F	C
Boreotrophon sp.															R	R					R
Adamnestia sp.															R						R
SCAPHOPODA																					
Laevidentalium? sp.																					F

to the *Vicaryella bacula*-*Cyclina* or *Cyclina* Assemblage of Shibata (1978).

Ie. *Cyclina* Assemblage: The *Cyclina* Assemblage is defined by the common occurrence of *Cyclina japonica* Kamada *in situ*, and associated with *Vicaryella "bacula"* (Yokoyama), *Tateiwaia* sp. nov., *Hiatula minoensis* (Yokoyama) and *Cerithideopsilla* aff. *minoensis* (Itoigawa). Difference from the *Dosinia*-*Cyclina*-*Vicaryella* Assemblage is indicated by the lack of *Dosinia* (*Phacosoma*) *kawagensis* Araki.

If. *Vicaryella*-*Tateiwaia* Assemblage: This assemblage is characterized by abundant occurrences of such gastropods as *Vicaryella "bacula"* (Yokoyama), *Tateiwaia* sp. nov. and *Vicaryella otukai* (Nomura), associated with a few other bivalve species. These species are crowded in dark gray mudstone.

Ig. *Cerithideopsilla*-*Dosinia* Assemblage: This assemblage consists of *Cerithideopsilla* aff. *minoensis* (Itoigawa), *Dosinia* (*Phacosoma*) *kawagensis* Araki, *Hiatula minoensis* (Yokoyama) and *Trapezium* (*Neotrapezium*) *modiolaeforme* Oyama and Saka and comes from muddy coarse-grained sandstone showing conspicuous bioturbation and included plant remains.

Type II: Type II is indicated by the occurrence of *Mya* sp., *Yoldia* (*Yoldia*) aff. *omorii* Aoki and *Boreotrophon* sp. in a massive muddy facies and by the lack of the main constituents of Type I.

IIa. *Nassarius-Yoldia* Assemblage: The *Nassarius-Yoldia* Assemblage is characterized by the common occurrence of *Nassarius* (*Zeuxis*) sp. in association with *Yoldia* (*Yoldia*) aff. *omorii* Aoki, *Mya* sp., *Boreotrophon* sp. and *Cultellus izumoensis izumoensis* (Yokoyama).

IIb. *Macoma* Assemblage: This assemblage is indicated by the sporadic occurrence of only three species; *Macoma* (*Macoma*) *incongrua* (v. Martens), *Mizuhopecten* aff. *chichibuensis mitsuganoensis* (Shibata) and *Mya* sp.

b. Paleoenvironment

The assemblages forming Type I involve *Ruditapes miyamurensis* (Itoigawa), *Nipponomarcia nakamurai* (Ikebe), *Hiatula minoensis* (Yokoyama), *Tateiwaia* sp. nov., and *Crassostrea gigas* (Thunberg) in addition to *Vicaryella* spp., *Cyclina japonica* Kamada, *Dosinia* (*Phacosoma*) *kawagensis* Araki and *Cerithideopsilla* aff. *minoensis* (Itoigawa). They are considered to have inhabited brackish to intertidal environments in an embayment. Of these assemblages, the *Nipponomarcia* and *Vicaryella-Tateiwaia* Assemblages are found in dark gray mudstone and the *Cyclina* Assemblage comes from tuffaceous siltstone, while the other assemblages are obtained from tuffaceous muddy sandstone.

On the other hand, Type II is characterized by *Mya* sp., *Yoldia* (*Yoldia*) aff. *omorii* Aoki and *Boreotrophon* sp., occurring in dark gray mudstone, and by lower richness and diversity than Type I. Except for *Nassarius* (*Zeuxis*) sp., *Macoma* (*Macoma*) *incongrua* (v. Martens) and *Clinocardium* sp., components of Type I are not found in Type II fauna. Therefore, it is evident that the elements of Type II lived at greater depth than Type I. Judging from the occurrences of *Mizuhopecten* aff. *chichibuensis mitsuganoensis* (Shibata), *Cultellus izumoensis izumoensis* Yokoyama and *Macoma* (*Macoma) incongrua* (v. Martens) in this type, the elements of Type II are likely to represent a middle to lower inner sublittoral muddy bottom environment.

The molluscan assemblages change from Type I to II vertically, except in the vicinity of the type locality of the Koiwai Mudstone, Sandstone and Conglomerate Member, where the change is not recognized. These facts indicate that the depositional environment of the member changes from brackish-intertidal to shallow sublittoral marine embayment environments in ascending order. Subsequently, the member was completely covered by pyroclastic deposits of the overlying Keiseitôge Andesite Member.

Characteristic of the molluscan fauna of the Yotsuyaku Formation and its significance

The molluscan fauna of the Yotsuyaku Formation has been considered equivalent to the Kadonosawa Fauna, as already mentioned. Otuka (1939) first designated as its type the molluscs from the lower part of his "Kadonosawa Series" studied by him (1934), and discussed its temporal and spatial distribution. He considered that the fauna was lower Miocene in age. The name "Kadonosawa Fauna" was used for the first time by Kanehara (1936), who discussed the temporal and spatial distribution of the "Ennichi (Yeongil) Fauna" of Korea, and pointed out that the fauna closely resembles the molluscan fauna of the "Kadonosawa Series" studied by Otuka (1934). Chinzei (1963, 1978, 1981a, b, 1983, 1986a, b), Tsuchi, *ed*. (1981) and Tsuchi and IGCP-114 National Working Group of Japan (1984) reviewed the distribution of the fauna with reference also to planktonic microfossil biostratigraphy and radiometric ages, and the Kadonosawa Fauna was considered to be restricted in its occurrence to the interval 16.5-15.0 Ma, or latest Early to early Middle Miocene. Thereafter, Itoigawa (1987, 1988) and Ogasawara (1988) revised the geological distribution of the fauna and suggested that the lower limit of the fauna may attain 19.0-18.5 Ma in several Pacific coast regions based on planktonic microfossil biostratigraphic and radiometric data.

In addition, Chinzei (1983, 1986a, b) revealed the northward succession of the Kadonosawa Fauna. He subdivided the distribution into three biogeographic provinces based on sublittoral taxa; tropical, subtropical and a mixed area with the temperate- to cold-water Chikubetsu Fauna. According to him, the first is characterized by *Telescopium, Geloina* and *Littorinopsis*, considered to be representatives of mangrove swamp dwellers as reported by Oyama (1950). The second is represented by the "Arcid-Potamid Fauna" (Tsuda, 1965; Noda, 1973), consisting of such genera as *Anadara* (*Hataiarca*), *Vicarya, Tateiwaia, Cerithideopsilla* and *Cerithidea*, with *Hiatula* and *Cyclina*. These genera also occur in the tropical province.

In the Tate Conglomeratic Sandstone Member of the Kadonosawa Formation, the type formation of the fauna, Chinzei and Iwasaki (1967) recognized *Batillaria, Ostrea, Dosinia-Clinocardium, Felaniella-Conus* and *Macoma* Assemblages and discussed their paleoecology. In addition, Matsubara (1995) reported on the occurrence of the "Arcid-Potamid Fauna" such as *Anadara* (*Hataiarca*) *kakehataensis* Hatai and Nisiyama, *Megaxinus khataii* (Otuka), *Cyclina japonica* Kamada, *Hiatula minoensis* (Yokoyama), *Vicaryella otukai* (Nomura), and *Tateiwaia* cf. *yamanarii* (Makiyama) from the member in Nisatai, Ninohe City. These components are included in the *Batillaria* Assemblage (Chinzei, 1981a, b). The *Batillaria* (= *Tateiwaia*; the writer's taxonomical ranking) Assemblage of Chinzei and Iwasaki (1967) is composed mainly of *Tateiwaia tateiwai* (Makiyama) or *T. yamanarii* (Makiyama), *Macoma* (*Macoma*) cf. *incongrua* (v. Marten), *Hiatula minoensis* (Yokoyama), *Megaxinus khataii* (Otuka), and *Ringicula ninohensis* Otuka. It occurs in a black muddy sandstone facies and is considered to inhabit a brackish lagoon or tidal flat environment. Consequently, it is believed that the *Hiatula, Tateiwaia, Dosinia-Cyclina-Vicaryella* and *Cerithideopsilla-Dosinia* Assemblages in Type I of the

Table 3. Specific comparisons of the constituents of the "Kadonosawa Fauna" between lower (left) and upper (right) horizons in selected districts. Data for each district is based on the following studies: Mizunami district; Itoigawa (1960), Itoigawa *et al.* (1974, 1981, 1982), Joban Coalfield; Kamada (1962, 1972), Takahashi (1984), Noda *et al.* (1989), Ninohe district; Otuka (1934), Chinzei and Iwasaki (1967), Chinzei (1979), Matsubara (1995 and unpublished data), Southwest Hokkaido; Uozumi and Fujie (1966), Kanno *et al.* (1988) and Suzuki *et al.* (1992, 1994).

DISTRICT	MIZUNAMI		JOBAN COAL-FIELD		NINOHE		SOUTHWEST HOKKAIDO	
GENUS/ FORMATION	TSUKIYOSHI	SHUKUNOHORA	KUNUGIDAIRA	NAKAYAMA	YOTSUYAKU	KADONOSAWA	YOSHIOKA	KUNNUI
Tateiwaia	sp. (=n. sp.)	*yamanarii*		*yamanarii* *tateiwai*	n. sp.	*yamanarii* *tateiwai*	cf. *yamanarii*	*yamanarii*
Vicaryella	*bacula* *ishiiana* *otukai*	*ancisa* (?)	*jobanica* *notoensis* (?)	*ishiiana* *notoensis*	"*bacula*" *otukai*	*ancisa* (=*atukoae*) *otukai*		*ishiiana*
Dosinia (*Phacosoma*)	*kawagensis* *nomurai*	*suketoensis* *nomurai*	*nomurai*	cf. *suketoensis* *nomurai*	*kawagensis*	*nomurai*		*nomurai*
Ruditapes	*miyamurensis*	*takagii*			*miyamurensis*	*takagii*		
Hiatula	*minoensis*	*minoensis*	*minoensis*	*minoensis*	*minoensis*	*minoensis*		*minoensis*
Nipponomarcia	*nakamurai*	*nakamurai*	*nakamurai*		*nakamurai*			*nakamurai*
Cyclina	*japonica*	*japonica*	*japonica* *lunulata*	*japonica*	*japonica*	*japonica* *lunulata*		*japonica*
Meretrix	*arugai*	*arugai*	*arugai*	*arugai*	*arugai*	*arugai* *ninohensis*		
Vicarya	*yokoyamai*	*yokoyamai*	*yokoyamai*	*yokoyamai*		*yokoyamai*		*yokoyamai*
Anadara (*Hataiarca*)		*daitokudoensis*		cf. *kakehataensis*		*kakehataensis*		*kakehataensis* "*kurosedaniensis*"

Yotsuyaku Formation faunas from the muddy sandstone facies correspond to the *Batillaria* Assemblage of the Kadonosawa Formation based on lithology and components.

Considering the comparison, the components of the Yotsuyaku Formation are characteristic in lacking not only tropical elements but also *Anadara* (*Hataiarca*) spp., characterizing the "Arcid Potamid Fauna", and composed of different species constituents to the Kadonosawa Fauna of Northeast Japan. For example, different species are recognized in such genera as *Tateiwaia, Vicaryella* and *Ruditapes*, whereas *Hiatula minoensis* (Yokoyama), *Meretrix arugai* Otuka, *Vicaryella otukai* (Nomura), and *Cyclina japonica* Kamada are found in both formations (Table 3).

In addition, it is noteworthy that *Nipponomarcia nakamurai* (Ikebe), *Dosinia* (*Phacosoma*) *kawagensis* Araki, *Ruditapes miyamurensis* (Itoigawa), *Trapezium* (*Neotrapezium*) *modiolaeforme* Oyama and Saka, *Tateiwaia* sp. nov. (=*Batillaria yamanarii* of Mizuno, 1964, from the Isomatsu Formation of Aomori Prefecture and *Tateiwaia* sp. of Itoigawa *et al.*, 1981 and 1982, from the Tsukiyoshi Member of the Akeyo Formation of Gifu Prefecture), and *Vicaryella "bacula"* (Yokoyama) are for the first time reported from the Yotsuyaku Formation, because these species show a pronounced resemblance to those of the lower part of the First Setouchi Miocene Series of Southwest Japan. They have been seldom reported from the Japan Sea side, nevertheless upper Lower-lower Middle Miocene deposits with the Kadonosawa Fauna are widely distributed (Figure 7-1). For example, in addition to reports from Southwest Japan, *Dosinia* (*Phacosoma*) *kawagensis* Araki has been reported only from the Ajiri Formation of Miyagi Prefecture and the Shiote Formation of Fukushima Prefecture (Masuda, 1963) in addition to the Sinhyeon Formation of Eoil district, Korea, where the species is associated with the "Arcid-Potamid Fauna" (Yoon, 1979) (Figure 7-2). However, co-occurrence of the present species in the "Arcid-Potamid Fauna" was not reported in the First Setouchi Miocene Series (Shibata, 1978; Itoigawa *et al.*, 1974, 1981, 1982), and its geographic areas very little overlap that of the "Arcid-Potamid Fauna" (Figures 7-1, 2).

Itoigawa (1987) proposed the Akeyo Fauna and emphasized that it is distinguished from the Kadonosawa Fauna (s.s.) (=the Kurosedani Fauna in his usage) on differences in its constituents, lacking typical tropical elements, and in its older geological age. He considered that the succession from the Akeyo to the Kurosedani Faunas occurred by shifting of warm currents around Southwest Japan, producing a change from subtropical to tropical marine conditions with migration in tropical elements. Detailed geological age determination of sequences in the First Setouchi Miocene Series yielding such molluscs is still unclear biostratigraphically in many districts. Saito (1963), Koizumi (1981) and Ibaraki (1981) studied the biostratigraphy of the upper part of the Mizunami Group and suggested that it correlates with the upper half of Zone N. 8 of Blow (1969) and the *Denticulopsis lauta* Zone. Yoshida (1987a, b, 1991) revealed that the age of the Awa, Ichishi, and Fujiwara Groups and the Chikusa Formation corresponds to Zone N. 7 and the lower half of Zone N. 8 based on planktonic foraminiferal biostratigraphy. In

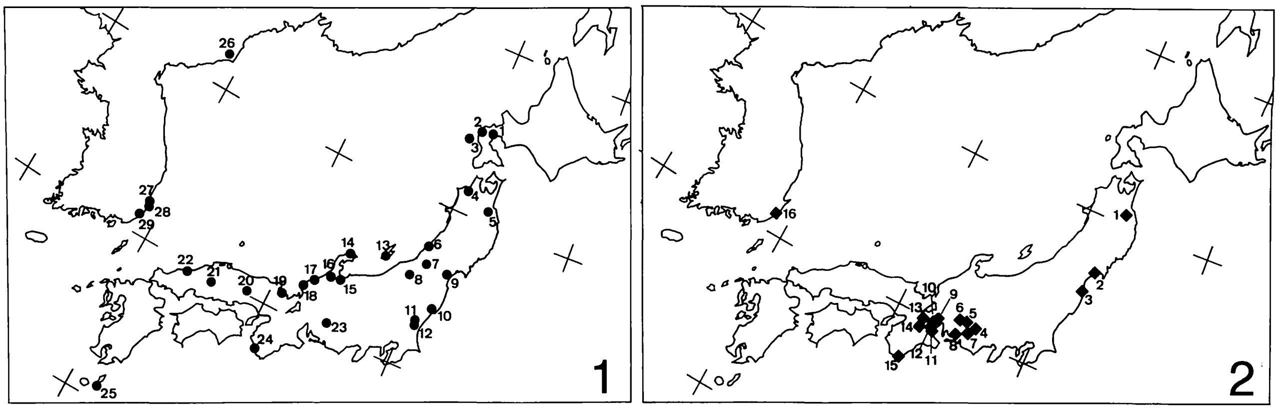

Figure 7. Comparison of the geographic distribution of the "Arcid-Potamid Fauna" and characteristic species of the Yotsuyaku Formation.

Fig. 7-1. Geographic distribution of *Anadara* (*Hataiarca*) spp. in latest Early-early Middle Miocene terms (modified from Noda and Takahashi, 1986). 1. Kunnui F. (Noda and Takahashi, 1986 ; Kanno *et al*., 1988), 2. Babagawa F. (Suzuki *et al*., 1994), 3. Tsurikake F. (Uozumi and Fujie, 1966), 4. Maenokawa F. (Iwai, 1960, 1965), 5. Kadonosawa F. (this study), 6. Oyama F. (Ogasawara and Nagasawa, 1992), 7. Myozawabashi F. (Sato *et al*., 1989), 8. Iwafune F. (Tsuda, 1965), 9. Tsukinoki F. (Ogasawara and Noda, 1978), 10. Nakayama F. (Takahashi, 1984), 11. Asagawa F. (Noda, 1973), 12. Tamagawa F. (Noda, 1973 ; Noda *et al*., 1994), 13. Orito F. (Kobayashi and Ueda, 1991), 14. Higashiinnai F. (Masuda, 1955, 1966), 15. Kurosedani F. (Hatai and Nisiyama, 1949 ; Tsuda, 1960), 16. Sunakozaka F. (Sasaki and Ogasawara, 1986), 17. Kawaminami F. (Bito *et al*., 1980), 18. Kunimi F. (Kaseno, 1956 ; Nakagawa, 1989), 19. Shimo F. of Uchiura Gr. (Nakagawa and Takeyama, 1985 ; Ozawa *et al*., 1986), 20. Yoshino F. of Katsuta Gr. (Taguchi, 1981), 21. Bihoku Gr. (Okamoto and Terachi, 1974 ; Taguchi *et al*., 1979), 22. Toyoda F. of Masuda Gr. (Takayasu, 1981), 23. Shukunohora Facies of Akeyo F. of Mizunami Gr. (Itoigawa *et al*., 1974, 1981, 1982 ; Okumura, 1983), 24. Kanayama F. (Yokoyama, 1923), 25. Kawachi F. of Kukinaga Gr. (Hayasaka, 1969), 26. Pyonryug F. of Meongcheon Gr. (Makiyama, 1926), 27. Cheongogsa F. in Pohang district (Yoon, 1976a, b ; Lee, 1992), 28. Songjeon F. in Eoil district (Kim *et al*., 1974 ; Lee, 1992), 29. Sinhyeon and Hwabongri Fs. in Ulsan district (Yoon, 1979 ; Lee, 1992).

Fig. 7-2. Geographic distribution of *Dosinia* (*Phacosoma*) *kawagensis* Araki.

1. Yotsuyaku F. (this study), 2. Ajiri F. (Masuda, 1963), 3. Shiote F. (Masuda, 1963), 4. Tomikusa Gr. (Shibata, 1978), 5. Tôyama F. of Mizunami Gr. (Shibata, 1978), 6. Akeyo F. of Mizunami Gr. (Itoigawa, 1955, 1960 ; Itoigawa *et al*., 1974, 1981, 1982), 7. Shitara Gr. (Shibata and Ina, 1983), 8. Okazaki F. (Hayashi and Miura, 1973), 9. Chikusa F. (Hata, 1967 ; Shibata, 1978), 10. Awa Gr. (Shibata, 1978), 11. Ichishi Gr. (Araki, 1960 ; Shibata, 1970, 1978), 12. Ayugawa Gr. (Shibata, 1978 ; Muramatsu, 1992), 13. Tsuzuki Gr. (Itoigawa, 1956 ; Shibata, 1978), 14. Yamabe Gr. (Shiida and Shibata, 1968), 15. Shimosato F. of Kumano Gr. (Honda *et al*., 1995), 16. Sinhyeon F. in Ulsan district, Korea (Yoon, 1979).

addition, Hayashida and Ito (1984) and Hayashida (1986) studied the paleo-magnetostratigraphy of the Ichishi and Mizunami Groups. They correlated the middle to upper part of the Ichishi Group and the Hongo and Akeyo Formations of the latter group to Epoch 16.

In Northeast Japan, similar stratigraphic differences in the shallow marine molluscan fauna of the upper Lower-lower Middle Miocene sequences have been pointed out in the Joban Coalfield of Fukushima Prefecture and southwest Hokkaido. For instance, in the Joban Coalfield, it is well known that *Vicarya* and *Vicaryella* species have been reported from two horizons separated by thick marine deposits. Kamada (1960, 1962, 1972) recorded these genera in the Kunugidaira Formation of the Yunagaya Group and the Nakayama Formation of the "Shirado Group" in ascending order, with each formation containing a different species of *Vicaryella*; *Vicaryella jobanica* Kamada in the former formation and *Vicaryella ishiiana* (Yokoyama) in the latter. Later, Takahashi (1984) for the first time reported the occurrence of the "Arcid-Potamid Fauna" in the Nakayama Formation. He also concluded that the *Vicarya* species occur in exactly the Kunugidaira and Nakayama Formations, and that the molluscs of the Kunugidaira Formation, lacking *Anadara* species, should be included in the "Ashiya Fauna". Masuda (1973) believed that the two formations accumulated in a short time and may be correlated with the formations yielding the Kadonosawa Fauna in other district. As a result of the development of planktonic microfossil biostratigraphy, the lower limit is still unidentified, but the geological age of the Yunagaya, "Shirado" and Takaku Groups in the Joban Coalfield is estimated to be 20 or 18 to 15 Ma (Koizumi, 1986a ; Yanagisawa *et al*., 1989 ; Taketani *et al*., 1990 ; Yanagisawa, 1993). Noda *et al*. (1989) examined molluscs from the Taki Formation (= the Kunugidaira Formation) and pointed out that the elements of this formation correspond to shallow embayment assemblages of the Kadonosawa Fauna, although lacking anadaran species. The Shiote Formation, noted above, is considered to be a correlative of the Kunugidaira

Formation (Fujita and Tsujikawa, 1960; Suzuki, 1963; Kubo *et al*., 1990).

Recently, Suzuki *et al.* (1992) briefly discussed the molluscan fauna of southwest Hokkaido and recognized three Miocene molluscan fossil stages; Yoshioka (18-17 Ma), Kunnui (16-15 Ma) and Yakumo Stages (12-7 Ma) in ascending order (Table 3). They considered the molluscan fauna of the first stage to be comparable with the Akeyo Fauna of Itoigawa (1987, 1988) and to indicate a warm to temperate climate based on the lack of subtropical elements such as *Vicarya* and *Vicaryella*, while the second stage is characterized by the "Arcid-Potamid Fauna".

The shallow marine molluscan fauna of the lower horizon of these two districts is characterized by lacking the "Arcid-Potamid Fauna" which is found only in the upper horizon as in the case of the First Setouchi Miocene Series and the Ninohe district. In addition, such changes have not been recognized in the reverse order. Considering these facts, the molluscan fauna of the Yotsuyaku Formation corresponds to the Akeyo Fauna of Southwest Japan and the Kadonosawa Fauna of Northeast Japan is also divided into the Akeyo and Kadonosawa Faunas (s.s.) stratigraphically.

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Postscript: After the manuscript was completed, the following studies treating the late Early to early Middle Miocene warm water molluscan fauna were published.

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Trans. Proc. Palaeont. Soc. Japan, N.S., No. 180, pp. 321-335, 5 Figs., December 30, 1995

1002 Fossil Mollusca of the Lower Miocene Yotsuyaku Formation in the Ninohe district, Iwate Prefecture, Northeast Japan

Part 2 (1). Bivalvia and Scaphopoda

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Abstract. Twenty species of Bivalvia and 1 species of Scaphopoda, obtained from the Koiwai Mudstone, Sandstone and Conglomerate Member of the Yotsuyaku Formation, are first described herein. Of these, one bivalve, *Trapezium* (*Neotrapezium*) *ichinohense*, is new to science.

Key words : Yotsuyaku Formation, Lower Miocene, Bivalvia, Scaphopoda, systematic description, *Trapezium* (*Neotrapezium*) *ichinohense* sp. nov.

Introduction

In this article and the following Part 2 (2), the writer describes molluscs from the Yotsuyaku Formation listed in Part 1 with revision of some species. The descriptions provide fundamental data for the conclusions reached in part 1. All specimens described and illustrated here are deposited in the Institute of Geology and Paleontology, Graduate School of Science, Tohoku University, under the IGPS (abbreviation for the institute) collection catalogue numbers.

Systematic descriptions and remarks

Class Bivalvia
Subclass Paleotaxodonta
Order Nuculoida
Family Nuculanidae
Genus **Yoldia** Möller, 1842
Subgenus **Yoldia** s.s.

***Yoldia* (*Yoldia*) aff. *omorii* Aoki, 1954**

Figures 1-2—4

Resembles.—
Yoldia omorii Aoki, 1954, p. 30, 31, pl. 2, fig. 18.
"*Nuculana omorii*" (Aoki). Uozumi, 1957, pl. 7, fig. 11.
Yoldia (*Yoldia*) omorii Aoki. Kamada, 1962, p. 59, pl. 2, figs. 17, 18.

Remarks.—Many poorly preserved specimens were obtained. They are characterized by a transversely elongated, small and poorly inflated shell with smoothly rounded anterior and slightly upturned, acutely angled rostrate posterior margins ; shell surface sculptured with close, fine concentric growth lines ; poorly elevated beak is situated at about the anterior two-fifths. The specimens closely resemble *Yoldia omorii* Aoki, 1954, originally described from the early Middle Miocene Kabeya Formation (=Numanouchi Formation of Kamada, 1962), Fukushima Prefecture. However, *Y. omorii* differs in having a beak situated centrally.

Locality.—14a (No. 102564), 14b, 19 (No. 102565).

Measurements (*in mm*).—

IGPS Coll. Cat. No.	Length	Height	Bp*	Bp/Length	Valve
102564	16.5	7.5	6.5	0.394	Right
102565-1	19.2	8.7	7.5	0.391	Left
102565-2	24.8	11.0	9.8	0.395	Left
102565-3	22.1	—	8.9	0.403	Right

*beak position fro anterior end

Subclass Pteriomorphia
Order Pterioida
Family Pectinidae
Genus **Mizuhopecten** Masuda, 1963

***Mizuhopecten* aff. *chichibuensis mitsuganoensis* (Shibata, 1970)**

Figures 1-11, 17a, b

Resembles.—
Patinopecten kobiyamai Kamada. Araki, 1960, p. 83, pl. 5, fig. 11. [not of Kamada, 1954]

Patinopecten (*Mizuhopecten*) *chichibuensis mitsuganoensis* Shibata, 1970, p. 63, 64, pl. 1, figs. 14a, b, pl. 2, figs. 1a, b.

Description.—Shell small in size, suborbicular, higher than long, subequilateral except for auricles, weakly inflated; apical angle about 70° on younger part, increasing to 90° with shell growth; shell surface sculptured with radial ribs and fine concentric growth lines; right valve with seven low, rounded radial ribs; interspaces nearly equal to or slightly narrower than ribs and flat-bottomed; fine distinct radial striae on crest and flanks of ribs; anterior and posterior ribs fine and bifurcated; anterior auricle longer than posterior and sculptured with five to seven radial threads and concentrical growth lines; byssal notch deep; posterior auricle inclines to anterior and sculptured by two or three radial ribs and fine concentric growth lines; left valve has five nearly flat-topped radial ribs that are narrower that their interspaces; interspaces sculptured with obtuse microscopic network; crest and flanks of ribs and interspaces ventrally carry fine radial threads; auricles as for right valve except for lack of byssal notch. Inner side of shell is not observed.

Remarks.—Single left and two right valves without shell material were obtained.

Comparison.—*Mizuhopecten chichibuensis mitsuganoensis* (Shibata, 1970), originally described from the Mitsugano Tuffaceous Sandstone and Shale Member of the Katada Formation, Ichishi Group of Mie Prefecture, resembles the present species, but is distinguished by possessing more elevated radial ribs on the left valve, an obtuse microscopic network over the whole of both valves, and smaller anterior auricles. The present species is similar to *"Kotorapecten" egregius* (Itoigawa, 1956) in having large anterior auricles and a deep byssal notch, but is distinguished by having fewer radial ribs. It also resembles *Mizuhopecten chichibuensis chichibuensis* (Kanno, 1957), described from the Nenokami Sandstone Member of the Ushikubitôge Formation in Saitama Prefecture, but differs in its smaller size, larger anterior auricle, deeper byssal notch on the right valve, and microscopic network only on interspaces of the left valve. *Mizuhopecten kobiyamai* (Kamada, 1954) is distinguished from the present species by possessing a larger shell, more inflated right valve, roof-topped radial ribs on the left valve, and imbricated radial threads on the ventral area.

Locality.—17 (No. 102568).

Measurements.—

IGPS Coll. Cat. No.	Length (mm)	Height (mm)	Apical angle (°)	Number of radial ribs	Valve
102568-1	32.5	36.1	92	7	Right
102568-2	32.5	33.9	90	5	Left
102568-3	16.4	17.8	95	7	Left

Family Anomiidae

Genus *Anomia* Linnaeus, 1758

Anomia chinesis Philippi, 1849

Figures 1-7a, b, 16a, b

Anomia chinensis Philippi. Kuroda, 1932, appendix p. 120; Habe, 1953, p. 198, 199, pl. 27, fig. 12, pl. 28, fig. 21; Hayasaka 1961, p. 33, pl. 3, fig. 7; Matsushima, 1969, pl. 10, fig. 4; Hayasaka, 1969, p. 42, pl. 2, figs. 3a, b; Kuroda *et al.*, 1971, p. 590, pl. 84, figs. 12-14, p. 378; Shibata in Itoigawa *et al.*, 1974, p. 71, pl. 15, figs. 5-7b; Ogasawara, 1976, p. 46, 47, pl. 1, fig. 19, pl. 4, fig. 9; Itoigawa *et al.*, 1981, 1982, p. 50, pl. 9, figs. 7a, b; Shibata and Ina, 1983, p. 42, pl. 4, fig. 8; Masuda *et al.*, 1983, p. 11, pl. 1, fig. 21; Ogasawara *et al.* eds., 1986, pl. 31, figs. 9a, b; Shibata *et al.*, 1987, pl. 1, fig. 3; Kobayashi, 1987, pl. 2, fig. 6; Baba, 1990, p. 257, pl. 28, fig 4; Masuda *et al.*, 1990, pl. 1, figs. 4A, B; Nakagawa *et al.*, 1993, p. 33, pl. 15, figs. 2a, b; Noda *et al.*, 1993, p. 143, 145, figs. 16-9a, b; Okumura and Takei, 1993, p. 167, pl. 35, fig. 7; Noda *et al.*, 1995, p. 59, figs. 7, 15 and 17-19.

Anomia cytaeum Gray. Yokoyama, 1920, p. 146, pl. 11, figs. 17a, b; Kuroda, 1932, appendix p. 120, fig. 122; Nomura, 1935a, p. 107, pl. 11, figs. 5, 6; Nomura and Hatai, 1936, p. 121; Nomura, 1938, p. 251, pl. 35, fig. 7; Nomura and Hatai, 1938, p. 49, 50; Nomura, 1940, p. 21, 22, pl. 2, fig. 14.

Anomia lischkei Dautzenberg and Fischer. Makiyama, 1927, p. 37; Kuroda, 1932, appendix p. 119, fig. 121; Ozaki, 1958,

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Figure 1. (All figures natural size, unless otherwise stated).

1a-b, 5. *Pillucina* (*Wallucina*) cf. *striata* (Tokunaga), Loc. 7, IGPS coll. cat. no. 102571, ×1.5, right valves. **2, 3, 4.** *Yoldia* (*Yoldia*) aff. *omorii* Aoki, 2: Loc. 14a, IGPS coll. cat. no. 102564, silicon rubber cast, right valve, 3: Loc. 19, IGPS coll. cat. no. 102565, left valve, 4: Loc. 19, IGPS coll. cat. no. 102565, silicon rubber cast, left valve (internal surface). **6, 22.** *Solen* sp., 6: Loc. 18, IGPS coll. cat. no. 102581, 22: Loc. 11, IGPS coll. cat. no. 102580, right valves. **7a-b, 16a-b.** *Anomia chinensis* Philippi, Loc. 13, IGPS coll. cat. no. 102569, left valves. **8.** *Felaniella ferruginata* (Makiyama), Loc. 15, IGPS coll. cat. no. 102574, left valve. **9, 10, 14, 15a-b.** *Macoma* (*Macoma*) *incongrua* (v. Martens), 9: Loc. 19, IGPS coll. cat. no. 102596, left valve, 10: Loc. 3, IGPS coll. cat. no. 102581, left valve, 14: Loc. 18, IGPS coll. cat. no. 102582, left valve, 15a-b: Loc. 12, IGPS coll. cat. no. 102583, 15a: Right valve, 15b: Left valve. **11, 17a-b.** *Mizuhopecten* aff. *chichibuensis mitsuganoensis* (Shibata), Loc. 17, IGPS coll. cat. no. 102568, 17a: silicon rubber cast, right valve, 11 and 17b: Left valves. **12, 18.** *Clinocardium* sp., Loc. 14b, IGPS coll. cat. no. 102576, silicon rubber cast, 12: Left valve, 18: Right valve. **13.** *Lucinoma* cf. *acutilineata* (Conrad), Loc. 14a, IGPS coll. cat. no. 102572, silicon rubber cast, right valve. **19.** *Cultellus izumoensis izumoensis* (Yokoyama), Loc. 14a, IGPS coll. cat. no. 102578, left valve. **20, 21.** *Hiatula minoensis* (Yokoyama), 20. Loc. 10, IGPS coll. cat. no. 102587, left valve, 21: Loc. 11, IGPS coll. cat. no. 102586, right valve. **23.** *Crassostrea gigas* (Thunberg), Loc. 10, IGPS coll. cat. no. 102566, left valve.


1a

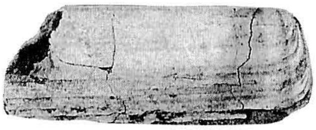

1b


2


3


4


5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7a


7b


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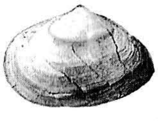
9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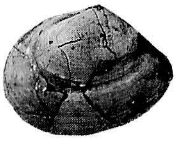
15a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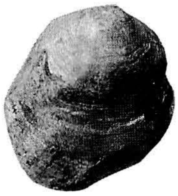
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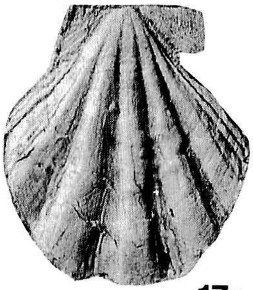
16b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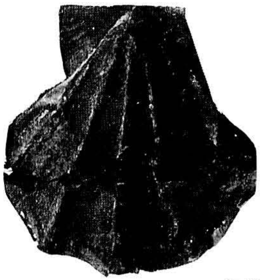
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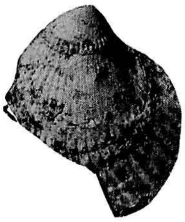
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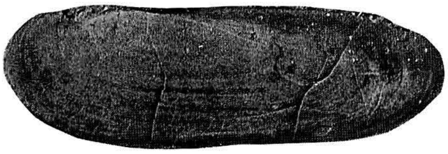
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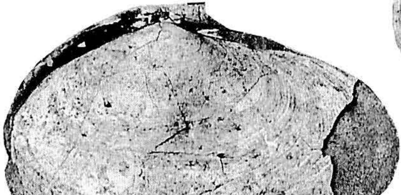
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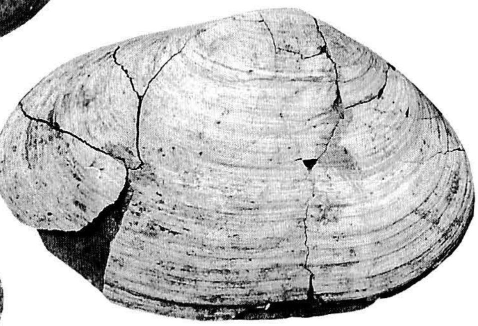
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22


23

p. 119, pl. 24, fig. 5 ; Kamada, 1962, p. 71, pl. 3, figs. 8-11.
Anomia nipponensis Yokoyama, 1920, p. 146, pl. 11, figs. 18a, b.

Remarks.—Several well preserved specimens were examined. *Anomia chinensis* from the Yotsuyaku Formation is characterized by its rather small size, suborbicular thin shell with the left valve moderately inflated. Inner side of left valve has an orbicular plug scar below the beak and two suborbicular adductor muscle scars arranging obliquely below the plug scar (as illustrated by Habe, 1953).

Locality.—5, 8a, 8b, 13 (No. 102569).

Distribution.—

Recent: South Hokkaido and more southern northeast Pacific coast.

Quaternary: Otanoshike F. in Hokkaido, Sasaoka F. in Akita Pref., Dainenji F. in Miyagi Pref., Omma F. in Ishikawa Pref., Kazusa Gr. in Chiba and Kanagawa Prefs., "Kozakai Mud" in Aichi Pref., Takahama Shell Bed in Fukui Pref.

Pliocene: Daishaka F. in Aomori Pref., Tatsunokuchi F. in Miyagi Pref., Hitachi and Kume Fs. in Ibaraki Pref., Kakegawa Gr. in Shizuoka Pref.

Middle Miocene: Utsuno F. in Yamagata Pref., Kubota F. in Fukushima Pref.

Upper Lower-lower Middle Miocene: Taira F. of the Yunagaya Gr. in Fukushima Pref., Ôshimojô and Arakida Fs. of the Tomikusa Gr. in Nagano Pref., Sunakozaka F. in Ishikawa Pref., Akeyo F. of the Mizunami Gr. in Gifu Pref., Kawakado and Shimoda Fs. of the Shitara Gr. in Aichi Pref., Nenobi Granule Conglomerate and Hiramatsu Sandstone and Siltstone Fs. of the Awa Gr. in Mie Pref., Okuyamada and Yuyantani Fs. of the Tsuzuki Gr. in Kyoto Pref., Kurokawa F. of the Ayugawa Gr. in Shiga Pref., "lower formation" of the Bihoku Gr. in Okayama and Hiroshima Prefs., Kawachi F. of the Kukinaga Gr. in Tanegashima Island, Kagoshima Pref.

Family Ostreidae
Genus **Crassostrea** Sacco, 1897

Crassostrea gigas (Thunberg, 1793)

Figures 1-23 ; 4-12

Ostrea gigas Thunberg. Tokunaga, 1906, p. 68, pl. 4, figs. 5a, b ; Yokoyama, 1920, p. 162, pl. 15, figs. 1, 2 ; Otuka, 1934, p. 610 ; Otuka, 1935, p. 885 ; Makiyama, 1936, p. 206, 207 ; Nomura and Ônisi, 1940, p. 182 ; Iwai and Siobara, 1969, pl. 1, figs. 14a, b, pl. 2, fig. 1.

Ostrea (*Crassostrea*) *gigas* Thunberg. Kuroda, 1930, appendix p. 55, 56, fig. 56 ; Nomura and Hatai, 1937, p. 126, 127, pl. 18, fig. 3 ; Hirayama, 1954, p. 57, 58 ; Habe, 1955, p. 8, 9, pl. 4, figs. 15, 16 ; Ozaki, 1958, p. 118, 119, pl. 21, fig. 7 ; Fujie, 1958, p. 35, pl. 27, figs. 22, 32 ; Hayasaka, 1960, pl. 38, figs. 1a, b, 2 ; Habe, 1960, p. 5, pl. 5, figs. 14, 15 ; Araki, 1960, p. 81, 82, pl. 11, figs. 1a, b ; Hayasaka, 1961, p. 34, 35 ; Oyama, 1973, p. 89, pl. 29, figs. 1, 4, pl. 30, figs. 2a, b ; Noda, 1973, pl. 5, fig. 6.

Ostrea gravitesta Yokoyama. Nomura, 1938, p. 248, 249, pl. 33, fig. 15. [not of Yokoyama, 1926b]

Crassostrea gigas (Thunberg). Habe, 1960, p. 5, pl. 5, figs. 14, 15 ; Matsushima, 1969, pl. 10, fig. 5 ; Kuroda *et al.*, 1971, p. 596, pl. 86, fig. 1, p. 382 ; Torigoe, 1981, p. 304, 305, pl. 2, fig. 1, pl. 14, figs. 1-7b, pl. 32, figs. 1, 2 ; Matsushima, 1982a, pl. 3, figs. 1, 2 ; Matsushima, 1982b, pl. 2, *fig. 6*, *pl.* 3, fig. 3 ; Amano, 1983, p. 43, pl. 2, figs. 2, 5 ; Masuda *et al.*, 1983, p. 11 ; Matsuura, 1985, pl. 33, figs. 9a, b ; Takayasu, 1985, pl. 2, figs. 11, 12a, b ; Takahashi, 1986, pl. 13, fig. 3 ; Kobayashi, 1987, pl. 2, fig. 18 ; Matsushima and Nara, 1987, pl. 1, figs. 1a, b, pl. 2, figs. 2a, b ; Matsukuma *et al.*, 1988, pl. 3, fig. 6 ; Nakagawa *et al.*, 1989, p. 33, 34, pl. 16, figs. 1a-d ; Baba, 1990, p. 262, pl. 29, fig. 9 ; Masuda *et al.*, 1990, pl. 1, fig. 3 ; Noda *et al.*, 1993, p. 145, 147, fig. 16-8 ; Amano, 1994, pl. 1, fig. 19.

Remarks.—Many well preserved specimens were obtained. Although those from the Yotsuyaku Formation are of medium size with a less inflated right valve possessing less elevated radial ridges compared with Recent specimens, these differences are considered to fall within the range of intraspecific variation for *C. gigas.*

Comparison.—*Crassostrea mundana* (Yokoyama, 1924), originally described from the Oligocene Iwaki Formation in the Joban Coalfield, closely resembles the present material, but is distinguished by possessing a broader ligamental groove and numerous finely undulating radial striae on the left (upper) valve. *Crassostrea gravitesta* (Yokoyama), a well known Miocene oyster from Japan and Korea, differs in its much larger size and robust, thick shell.

Locality.—1, 3, 4, 5, 6, 7, 8a, 8b, 10 (No. 102566), 11 (No. 102595), 12, 13, 15, 18 (No. 102567).

Distribution.—This species is distributed throughout the coast of Sakhalin, Japan, Korea, China and Southeast Asia in the Recent (Trigoe, 1981), and there are many fossil records from Lower Miocene and younger strata around Japan and in several districts of Korea. From upper Lower-lower Middle Miocene sequences, it is known from the following: Kadonosawa and Suenomatsuyama Fs. in Iwate Pref., Kanagase F. in Miyagi Pref., Kobana F. of the Arakawa Gr. in Tochigi Pref., Ôshimojô and Arakida Fs. of the Tomikusa Gr. in Nagano Pref., Ochiai Facies and Ôi F. of the Ichishi Gr., Hiramatsu Sandstone and Siltstone F. of the Awa Gr. in Mie Pref., Okuyamada and Yuantani Fs. of the Tsuzuki Gr. in Kyoto Pref., Lower Manhondong (Mankodô) F. of the Meongcheon (Meisen) Gr. in North Korea.

Subclass Heterodonta
Order Veneroida
Family Lucinidae
Genus **Pillucina** Pilsbry, 1921
Subgenus **Wallucina** Iredale, 1930

Pillucina (**Wallucina**) cf. **striata** (Tokunaga, 1906)

Figures 1-1a, b, 5 ; 2

Compared with.—

Lasaea striata Tokunaga, 1906, p. 53, 54, pl. 3, figs. 14a, b.
Lucina contraria Dunker. Yokoyama, 1920, p. 134, pl. 10, fig. 8
? *Pillucina contraria* (Dunker). Otuka, 1934, p. 616, pl. 48, figs.

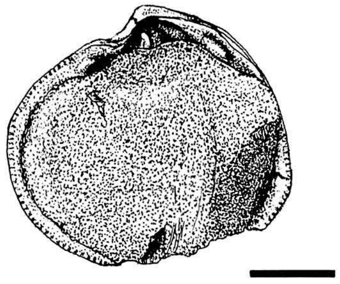


Figure 2. Hinge area and inner margin of right valve of *Pillucina* (*Wallucina*) cf. *striata* (Tokunaga) from the Yotsuyaku Formation (IGPS coll. cat. no. 102571). Same specimen as Figures 1-1a, b. Scale bar = 2 mm.

37, 38.

"Lucina" contraria Dunker. Otuka, 1935, p. 892, pl. 57, figs. 190, 191

Wallucina lamyi Chavan. Yamamoto and Habe, 1959, p. 91, pl. 6, figs. 28, 29; Hayasaka, 1961, p. 40, pl. 4, figs. 4a, b; Yoon, 1988, pl. 1, figs. 18-20; Ogasawara *et al*. eds., 1986, pl. 72, figs. 2a-c.

Pillucina (*Wallucina*) *lamyi* (Chavan). Kaseno and Matsuura, 1965, pl. 13, fig. 3.

Pillucina (*Wallucina*) *striata* (Tokunaga). Kuroda *et al*., 1971, p. 611, pl. 118, fig. 15, p. 392; Oyama, 1973, p. 69, pl. 40, figs. 3a, b; Matsuura, 1977, pl. 3, fig. 15; Ogasawara *et al*. eds., 1986, pl. 72, figs. 3a, b.

Pillucina striata (Tokunaga). Baba, 1990, p. 263, pl. 29, fig. 12.

Remarks.—The specimens from the Yotsuyaku Formation are characterized by the following features: shell of small size, suborbicular or subtrigonal in form, inequilateral, moderately inflated; rather distinct keel extends from beak to posteroventral margin; anterior margin well rounded; posterior margin subtruncate; shell surface sculptured with concentric growth lines and numerous microscopic radial threads over the whole surface; lunule small but well impressed; inner margin finely crenulated except along hinge plate. As shown in Figure 2, the hinge area of the right valve possesses a strong subtrigonal tooth and nodulous, strongly elevated anterior and posterior lateral teeth.

Comparison.—The specimens closely resemble *Pillucina* (*W.*) *striata* (Tokunaga, 1906), a living species, but are distinguished by having a more inflated shell. *Pillucina* (*Wallucina*) *habei* (Itoigawa, 1955b), originally described from the Kubohara Sandstone Member of the Tôyama Formation of the Mizunami Group in Gifu Prefecture, resembles the present species, but is distinguished by possessing a higher shell with a less produced anterior margin. *Pillucina* (*Wallucina*) *okumurai* proposed by Itoigawa (1957) may be distinguished from the present species by having a less truncated posterodorsal margin.

Locality.—2 (No. 102570), 7 (No. 102571).

Genus *Lucinoma* Dall, 1901

Lucinoma cf. *acutilineata* (Conrad, 1849)

Figure 1-13

Compared with.—

Lucina acutilineata Conrad. Otuka, 1934, p. 614; Hatai, 1940, p. 125; Nomura and Ônisi, 1940, pl. 17, figs. 9-12.

Lucina (*Myrtea*) *acutilineata* Conrad. Nomura, 1935a, p. 76-79; Nomura 1935b, p. 109, 110, pl. 5, figs. 1, 2; Nomura and Zimbô, 1935, p. 10; Nomura, 1935c, p. 53; Nomura, 1935d, p. 210, 211; Nomura and Hatai, 1936, p. 123.

Lucina (*Lucinoma*) *acutilineata* Conrad. Otuka, 1935, p. 892.

Lucinoma acutilineatum (Conrad). Shikama, 1954, pl. 5, fig. 2; Aoki, 1959, p. 268, pl. 1, fig. 14; Iwai, 1961, pl. 1, fig. 10; Kamada, 1962, p. 95-97, pl. 9, figs. 10-16, pl. 10, figs. 1-3; Ogasawara, 1976, p. 48, 49, pl. 4, fig. 12; Yoon, 1976a, p. 10, 11, pl. 3, figs. 10, 11, 14; Kim and Yoon, 1978, p. 6, 7, pl. 1, figs. 1, 2; Ogasawara and Yashima, 1981, pl. 3, figs. 7a, b; Itoigawa *et al*., 1981, 1982, p. 68, pl. 12, figs. 13a, b; Educ. Comm. Fukushima Pref. eds., 1983, pl. 1, figs. 9-13; Shibata and Ina, 1983, p. 46, pl. 5, fig. 9; Tsuru, 1983, p. 59, 60, pl. 9, figs. 11, 12; Matsuura, 1985, pl. 34, fig. 15; Takahashi, 1986, pl. 14, fig. 2; Ogasawara *et al*. eds., 1986, pl. 12, figs. 4, 7, 10, pl. 14, figs. 10, 12a-c, 14; Kobayashi, 1986, pl. 21, fig. 14; Ogasawara *et al*., 1989a, pl. 1, fig. 10; Ogasawara *et al*., 1989b, pl. 2, figs. 7a-b.

Lucinoma acutilineata (Conrad). Hirayama, 1954, p. 60-62, figs. 2-7; Itoigawa, 1955, pl. 6, fig. 4; Hirayama, 1956, p. 108, pl. 6, fig. 8; Itoigawa, 1956, pl. 2, fig. 2; Itoigawa, 1957, p. 4, 5, pl. 1, figs. 9-11; Ozaki, 1958, p. 125, pl. 18, figs. 11, 12, ? pl. 21, fig. 3, pl. 23, fig. 4; Kanno and Akatsu, 1972, pl. 8, fig. 16; Itoigawa in Itoigawa *et al*., 1974, p. 76, 77, pl. 19, figs. 6-10c; Amano, 1983, p. 45, pl. 5, fig. 5, pl. 9, figs. 11, 12; O'Hara and Nemoto, 1984, pl. 1, fig. 10; Matsui, 1985, p. 230, pl. 32, fig. 10; Itoigawa and Shibata, 1986, pl. 17, fig. 12; Noda and Amano, 1986, pl. 4, figs. 1a-2, pl. 5, figs. 9, 10; Marincovich, 1988, p. 10, 11, pl. 1, figs. 2a, b; Kanno *et al*., 1988, pl. 2, figs. 5, 6; Baba, 1990, p. 264, pl. 30, fig. 1; Matsui, 1990, fig. 5-2; Noda, 1992, p. 65, pl. 1, figs. 20-23; Muramatsu, 1992, pl. 49, fig. 5; Lee, 1992, p. 81, fig. 26-19; Noda and Hoyanagi, 1993, fig. 9-4; Noda *et al*., 1995, p. 61, 62, figs. 9-5, 6 and 16-18-21 (? fig. 16, 17).

not *Lucina* (*Myrtea*) *acutilineata* Conrad. Nomura and Hatai, 1935, p. 9, 10, pl. 2, figs. 3, 4. [*Lucinoma annulata* (Reeve)]

not *Lucina* (*Lucinoma*) *acutilineata* Conrad. Nomura, 1938, p. 253, pl. 35, fig. 5. [*Lucinoma annulata* (Reeve)]

Remarks.—Several poorly preserved, compressed specimens were obtained. They have a small suborbicular shell with subtruncated posterior; the surface is sculptured with fine and lamellar concentric ribs and a few fine striae on each interspace. Features of the lunule and shell interior were not observed.

Locality.—14a (No. 102572), 14b (No. 102573), 16.

Family Ungulinidae
Genus *Felaniella* Dall, 1899

Felaniella ferruginata (Makiyama, 1926)

Figures 1-8; 3

Diplodonta ferruginata Makiyama, 1926, p. 157, 158, pl. 12, figs. 12, 13; Makiyama, 1936, p. 208; Araki, 1960, p. 89, pl. 6, figs. 8, 9; Mizuno, 1964, pl. 2, fig. 6; Uozumi and Fujie, 1966, p. 150, pl. 6, figs. 8, 9; Itoigawa in Itoigawa *et al.*, 1974, p. 76, pl. 19, figs. 5a-c; Itoigawa *et al.*, 1981, 1982, p. 70, pl. 12, figs. 8a, b, 11a, b; Ogasawara and Nagasawa, 1992, p. 1233, 1235, figs. 7-6a-c, -7a-c, -8.

Taras ferruginata (Makiyama). Otuka, 1934, p. 616, pl. 47, fig. 35, pl. 38, figs. 39, 40.

Felaniella (*Felaniella*) *ferruginata* (Makiyama). Yoon, 1976a, p. 11, pl. 2, figs. 15, 16; Yoon, 1979, p. 12, pl. 4, fig. 2; Lee, 1992, p. 83, 84, figs. 24-23-28.

Felaniella ferruginata (Makiyama). Sasaki and Ogasawara, 1986, pl. 5, fig. 10; Kobayashi and Ueda, 1991, p. 134, 135, pl. 3, figs. 7, 8.

? *Diplodonta ferruginata* Makiyama. Nakagawa and Takeyama, 1985, pl. 17, fig. 1; Ozawa *et al.*, 1986, pl. 14, fig. 1. [? *Cycladicama takeyamai* (Otuka)]

? *Felaniella ferruginata* (Makiyama). Nakagawa, 1989, p. 37, pl. 1, fig. 9.

not *Cycladicama ferruginatum* (Makiyama). Oyama *et al.*, 1994, p. 23, 24. [*Cycladicama takeyamai* (Otuka)]

Remarks.—A small articulated specimen was obtained. *Felaniella ferruginata* is characterized by its small size, slighty longer than high, anteriorly inclined inequilateral inflated shell with short and narrowly arcuate anterior margin, straight posterodorsal margin which is parallel to the posteroventral margin, and a subtruncated posterior. Although the generic position of this species has been controversial, the writer considers that it belongs to the genus *Felaniella* Dall (1899) because of the morphology of the anterior adductor muscle scar, whose inner margin is irregularly undulating (Figure 3), as revised in Yoon (1976a).

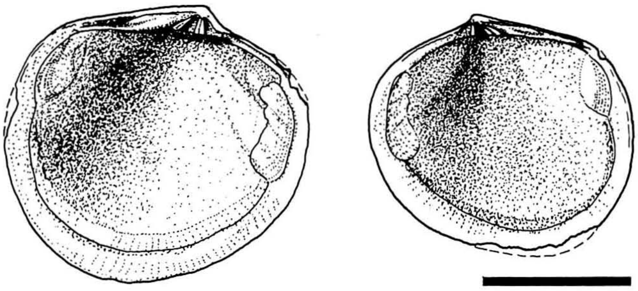


Figure 3. Inner surfaces of *Felaniella ferruginata* (Makiyama) from the Tate Conglomeratic Sandstone Member of the Kadonosawa Formation at Nisatai, Ninohe City, Iwate Prefecture (IGPS coll. cat. no. 102575). Note especially the morphology of the anterior adductor muscle scars. Scale bar=10 mm.

Comparison.—*Felaniella usta* (Gould), a Miocene to Recent species, differs in having a more orbicular, more equilateral shell. Recently, Oyama *et al.* (1994) considered *Cycladicama takeyamai* (Otuka, 1938) to be a synonym of the present species as a result of their reexamination of topotype specimens. They were unfortunately not illustrated, but it seems that that species is less inflated and more orbicular. Furthermore, the morphological features of the anterior adductor muscle scar of *C. takeyamai* have not been described or illustated. Consequently, the present writer regards these two species as not conspecific.

Locality.—15 (No. 102574).

Distribution.—Tsurikake F. in Hokkaido, Isomatsu F. in Aomori Pref., Kadonosawa F. in Iwate Pref., Nakayama F. in Fukushima Pref., Oyama F. in Yamagata Pref., Orito F. in Niigata Pref., Higashi-innai and Sunakozaka Fs. in Ishikawa Pref., Shimo F. of the Uchiura Gr. in Fukui Pref., Akeyo and Oidawara Fs. of the Mizunami Group in Gifu Pref., Kaisekizan F. of the Ichishi Gr. of Mie Pref., Korematsu F. of the Bihoku Gr. in Hiroshima Pref., Japan. Cheongogsa, Sinhyeon and Manhongdong (Mankodô) Fs., Korea.

Family Cardiidae
Genus *Clinocardium* Keen, 1936

Clinocardium sp. indet.

Figures 1-12, 18

Remarks.—Although *Clinocardium* in the Yotsuyaku Formation was listed by Hayakawa *et al.* (1954) and Chinzei (1958a) as *Clinocardium shinjiense* (Yokoyama, 1923a), this writer does not consider this to be a sound identification because *Clinocardium* from this formation has quadrate radial ribs whose width is nearly equal to or slightly narrower that their interspaces and numbering more than 23, while *C. shinjiense* has roof-topped or rounded ones. Specific identification is difficult because the number of ribs is uncertain.

Locality.—1, 2, 14a, 14b (No. 102576), 19 (No. 102577).

Family Tellinidae
Genus *Macoma* Leach, 1819
Subgenus *Macoma* s.s.

Macoma (***Macoma***) ***incongrua*** (v. Martens, 1865)

Figures 1-9, 10, 14, 15a, b

Tellina incongrua v. Martens, 1865, p. 430 (*non vidi, fide* Ôinomikado, 1934).

Macoma dissimilis (v. Martens). Yokoyama, 1920, p. 116, 117, pl. 7, figs. 19a-20.

Macoma inquinata Deshayes. Yokoyama, 1920, p. 117, pl. 8, figs. 1, 2.

Macoma incongrua (v. Martens). Ôinomikado, 1934, text-figs. 8, 9, pl. 8, figs. 16, 17; Nomura, 1935c, p. 61, 62; Nomura, 1935d, p. 218, 219; Nomura and Hatai, 1936, p. 130; Habe, 1955, p. 18, pl. 3, fig. 6; Yamamoto and Habe, 1959, p. 104, 105, pl. 9, fig. 3, pl. 14, figs. 25, 26; Chinzei, 1959, text-figs. 3, 4; Kanno and Ogawa, 1964, pl. 1, fig. 12; Matsushima, 1969, pl. 11, fig. 9; Iwasaki, 1970, p. 410, 411, pl. 1, fig. 14; Oyama, 1973, p. 113, pl. 52, figs. 9, 11-13; Kobayashi, 1987, pl. 3, figs. 7a, b; Okumura and Koyanagi, 1989, p. 77, pl. 8, fig. 11; Baba, 1990, p. 286, pl. 35, fig. 2; Noda, 1992, p. 80, pl. 6, figs. 4a, b.

Macoma (*Macoma*) *incongrua* (v. Martens). Hayasaka, 1961, p. 58; Amano, 1980, p. 109, pl. 13, fig. 25; Amano, 1983, p. 55, pl. 7, figs. 1a, b; Matsuura, 1985, pl. 33, fig. 16; Takahashi, 1986, pl. 14, fig. 8; Nakagawa *et al*., 1989, p. 40, pl. 28, fig. 4; Nakada and Amano, 1991, pl. 5, fig. 21; ? Lee, 1992, p. 86, figs. 28-6-9.

Remarks.—*Macoma* (*Macoma*) *incongrua* is characterized by its small size, with the beak situated rather posteriorly, and with a very weakly rounded posterodorsal margin.

Comparison.—*Macoma* (*Macoma*) *tokyoensis* Makiyama, 1927, a living species, rather resembles the present species, but is distinguished by its larger shell with a straighter posterodorsal margin and a more elevated and produced umbonal area.

Locality.—3 (No. 102581), 5, 6, 7, 10, 12 (No. 102583), 17, 18 (No. 102582), 19 (No. 102596).

Distribution.—

Recent: China, Korea, Japan, Maritime Prov. of Russia, and Alaska (Habe, 1955).

Quaternary: Otanoshike F. of Hokkaido, Kazusa Gr. in Chiba and Kanagawa Prefs., "Toshima Sand" of the Toyohashi Gr. in Aichi Pref., Takahama Shell Bed in Fukui Pref.

Pliocene: Kume F. in Ibaraki Pref., Seguchi F. in Nagano Pref., Ashigara Gr. in Kanagawa and Shizuoka Prefs.

Middle-Late Miocene: Togeshita F. in Hokkaido, Kubota F. in Fukushima Pref.

Late Early-early Middle Miocene: Chikubetsu, Yudoro and Takinoue Fs. of Hokkaido, Tanosawa F. in Aomori Pref., Ajiri F. in Miyagi Pref., Japan. Duho and Cheongogsa Fs. in the Pohang district, Korea.

Family Psammobiidae
Genus **Hiatula** Modeer, 1793

Hiatula minoensis (Yokoyama, 1926)

Figures 1-20, 21

Soletellina minoensis Yokoyama, 1926a, p. 221, pl. 28, figs. 13-16; Otuka, 1938, pl. 2, figs. 14, 18; Masuda, 1955, pl. 19, fig. 9; Araki, 1960, p. 100, pl. 8, fig. 1; Kamada, 1962, p. 126, 127, pl. 14, fig. 7; Mizuno, 1964, pl. 4, figs. 3, 4; Mizuno, 1965, p. 332, pl. 1, fig. 3; Uozumi and Fujie, 1966, pl. 12, fig. 12; Hayashi and Miura, 1973, pl. 2, figs. 19, 20; Kim *et al*., 1974, p. 278, pl. 3, fig. 4; Okamoto and Terachi, 1974, pl. 47, fig. 9; Yoon, 1979, p. 14, pl. 4, figs. 5, 7, 9; O'Hara and Nemoto, 1984, pl. 1, fig. 17; Kanno *et al*., 1988, pl. 1, fig. 10.

Sanguinolaria (*Soletellina*) *minoensis* (Yokoyama). Otuka, 1934, p. 619, pl. 49, figs. 65a, b; Otuka, 1938, p. 34; Oyama and Saka, 1944, p. 141, pl. 15, figs. 17, 18 (misspelled as *Sanguinorari*).

Sanguinolaria minoensis (Yokoyama). Makiyama, 1958, pl. 39, figs. 13-16.

Hiatula minoensis (Yokoyama). Itoigawa in Itoigawa *et al*., 1974, p. 96, pl. 28 figs. 10-11b; Itoigawa and Nishikawa, 1976, pl. 34, fig. 10; Taguchi *et al*., 1979, pl. 3, fig. 4; Taguchi, 1981, pl. 2, fig. 12; Itoigawa *et al*., 1981, 1982, p. 20, pl. 20, figs. 1a, b; Shibata and Ina, 1983, p. 51, pl. 7, fig. 4; Okamoto *et al*., 1983, pl. 23, figs. 31, 32; Nakagawa and Takeyama, 1985, pl. 17, fig. 11; Ozawa *et al*., 1986, pl. 14, fig. 4; Nakagawa, 1989, pl. 2, figs. 3a, b; Okamoto *et al*., 1989, pl. 6, figs. 17, 18; Iwamura Research Group, 1989, pl. 21, fig. 4; Shibata and Kato, 1988, pl. 3, fig. 14; Okamoto *et al*., 1990, pl. 9, fig. 29; Lee, 1992, p. 86, figs. 31-4, 5, -14: Ogasawara and Nagasawa, 1992, p. 1241, figs. 8-1a, b, -2a, b, -5, -6a, b, 9-27; Amano, 1992, pl. 57, fig. 14; Noda *et al*., 1994, figs. 6-8, -11, -16.

Soletellina cf. *minoensis* Yokoyama. Kaseno, 1956, p. 6, pl. 3, figs. 14a-c.

Remarks.—*Hiatula minoensis* is characterized by a moderate-sized shell which is moderately inflated and transversely elongate-oval in form with a weakly elevated beak situated rather anteriorly.

Locality.—2 (No. 102586), 4, 5 (No. 102585), 7, 8a, 8b, 9, 10 (No. 102587), 11 (No. 102588), 12, 18 (No. 102610).

Distribution.—Kunnui and Tsurikake Fs. of Hokkaido, Isomatsu and Nagane Fs. in Aomori Pref., Kadonosawa F. in Iwate Pref., Shimonagasawa F. in Akita Pref., Myozawabashi, Hondoji and Oyama Fs. in Yamagata Pref., Ajiri and Tsukinoki Fs. in Miyagi Pref., Shiote F. and Kunugidaira and Goyasu Fs. of the Yunagaya Gr. and Nakayama F. in Fukushima Pref., Tamagawa F. in Ibaraki Pref., Kozono F. in Saitama Pref., Orito F. in Niigata Pref., Kurosedani F. in Toyama Pref., Kawaminami, Sunakozaka and Higashiinnai Fs. in Ishikawa Pref., Aoki and Omi Fs., and Ôshimojô and Arakida Fs. of the Tomikusa Gr. in Nagano Pref., Kawakado F. of the Shitara Gr. and Okazaki F. in Aichi Pref., Tôyama and Akeyo Fs. of the Mizunami Gr. in Gifu Pref., Hiramatsu Sandstone and Siltstone F. of the Awa Gr. and Kaisekizan F. of the Ichishi Gr. in Mie Pref., Okuyamada F. of the Tsuzuki Gr. in Kyoto Pref., Kunimi F., and Shimo F. of the Uchiura Gr. in Fukui Pref., Yoshino F. of the Katsuta Gr. in Okayama Pref., Bihoku Gr. in Hiroshima Pref., Hirashima Conglomerate F. of the Susa Gr. in Yamaguchi Pref., Japan. Cheongogsa and Hagjeon Fs. in the Pohang district, Sinhyeon F. in the Ulsan district, Eoil and Songjeon Fs. in the Eoil district, and Pyonryug (Heiroku) F. of the Meongcheon (Meisen) Gr. in the Meongcheon district, Korea.

Family Solenidae
Genus **Solen** Linnaeus, 1758

Solen sp. indet.

Figures 1-6, 22

Remarks.—This species is characterized by its compressed elongated cylindrical shell with straight and parallel postumbonal dorsoventral margins and rounded anterior and posterior corners. The features of obliquely truncated anterior end and vertically subtruncated posterior one closely resemble *Solen krusensterni* Schrenk, a living species, which differs from the present species in having an upwardly recurved posterior margin.

Locality.—1, 2, 5, 7, 10, 11 (No. 102580), 12, 18 (No. 102581).

Family Cultellidae
Genus ***Cultellus*** Schumacher, 1817

Cultellus izumoensis izumoensis Yokoyama, 1923

Figure 1-19

Cultellus izumoensis Yokoyama, 1923a, p. 5, pl. 2, figs. 1a, b; Nomura, 1935d, p. 220, pl. 16; Nomura and Hatai, 1936, p. 132; Otuka, 1941, p. 23, 24, fig. 4; Kanno, 1956, p. 213, 214, pl. 5, fig. 8; Iwai, 1961, pl. 1, fig. 19; Iwai, 1965, p. 45, pl. 12, fig. 15; Uozumi and Fujie, 1966, p. 153, pl. 121, fig. 7; Hata, 1967, pl. 4, fig. 17; Hayashi and Miura, 1973, pl. 1, fig. 22; Itoigawa in Itoigawa *et al.*, 1974, p. 101, pl. 31, figs. 4, 5; Shibata and Kato, 1975, pl. 16, fig. 23; Ogasawara, 1976, p. 57, pl. 14, figs. 16, 18; Yoon, 1979, p. 13, pl. 4, fig. 8; Taguchi *et al.*, 1979, pl. 3, fig. 5; Ogasawara and Nomura, 1980, p. 89, pl. 11, figs. 5a, b, 9; Bito *et al.*, 1980, pl. 3, fig. 19; Taguchi, 1981, pl. 2, figs. 13, 14; Takayasu, 1981, p. 102, 103, pl. 3, figs. 10, 11; Itoigawa, 1981, 1982, p. 104, pl. 20, figs. 3a, b; Shibata and Ina, 1983, p. 52, pl. 7, fig. 2; Chijiwa and Tomita, 1985, pl. 41, fig. 1; Nakagawa and Takeyama, 1985, pl. 18, fig. 5; Shibata *et al.*, 1987, pl. 1, fig. 15; Shibata and Kato, 1988, p. 28, 29, pl. 3, figs. 10, 11; Nakagawa, 1989, pl. 1, fig. 10; Noda *et al.*, 1989, pl. 25, fig. 10; Ogasawara and Nagasawa, 1992, p. 1241, figs. 8-9a-c, -10, -13a-c, 9-29; Noda, 1992, p. 77, 78.

Phaxas cf. *izumoensis* (Yokoyama). Masuda, 1955, pl. 19, figs. 14a, b.

Cultellus izumoensis izumoensis Yokoyama. Amano, 1980, p. 110, 111, pl. 13, fig. 23.

Cultellus (*Cultellus*) *izumoensis* Yokoyama. Lee, 1992, p. 87, figs. 31-8, -16.

Cultellus otukai Ogasawara and Tanai, 1952, p. 211, pl. 19, fig. 19; Kanno, 1956, p. 216, pl. 6, figs. 9-12; Aoki, 1959, p. 274, pl. 3, figs. 33, 34; Kanno, 1960, p. 306, 307, pl. 44, figs. 12a, b, 13.

? *Cultellus izumoensis* Yokoyama. Katto and Masuda, 1978, pl. 3, figs. 8, 9. [? *Adulomya* sp.]

? *Cultellus* (*Cultellus*) *otukai* Ogasawara and Tanai. Lee, 1992, p. 87, fig. 31-6.

Remarks.—Several specimens lacking shell material were examined. Specimens from the Yotsuyaku Formation possess rather smaller shells with the posterodorsal and posteroventral margins parallel, a rounded posterior, and the beak at the anterior three-tenths.

As already pointed out by Ogasawara and Nagasawa (1992), *C. otukai*, described by Ogasawara and Tanai (1952) from the Oyama Formation in Yamagata Prefecture, is considered to be conspecific with *C. izumoensis izumoensis*.

Locality.—14a (No. 102578), 14b, 19.

Distribution.—Chikubetsu, Takinoue, Yudoro and Tsurikake Fs. of Hokkaido, Sunakose, Tanosawa and Takahoko Fs. in Aomori Prefecture, Kadonosawa and Suenomatsuyama Fs. in Iwate Pref., Ajiri F. in Miyagi Pref., Oyama F. in Yamagata Pref., Kunugidaira F. in Fukushima Pref., ? Higashiinnai F. in Ishikawa Pref., Uchiyama F. in Gumma Pref., Ushikubitoge and Nagura Fs. in Saitama Pref., Akamata Sandstone and Towata Mudstone Fs. of the Kurami Gr. and Oga F. in Shizuoka Pref., Aoki and Omi Fs., Neba, F., and Nukuta F. of the Tomikusa Gr. in Nagano Pref., Kawakado and Shimoda Fs. of the Shitara Gr. and Okazaki F. in Aichi Pref., Tôyama and Akeyo Fs. of the Mizunami Gr. in Gifu Pref., Kunimi F., and Shimo F. of the Uchiura Gr. in Fukui Pref., Toyoda F. of the Masuda Gr. and Fujina F. in Shimane Pref., ? Uematsu F. of the Muro Gr. in Wakayama Pref., "lower formation" of the Bihoku Gr. in Hiroshima Pref., Japan. Sinhyeon F. in the Ulsan district and Hagjeon F. in the Pohang district, Korea.

Measurements (*in mm*).—

IGPS Coll. Cat. No.	Length	Height	*Bp	Bp/Length	Valve
102578	56.8	16.6	17.0	0.299	Left

*Beak position from anterior end

Family Trapeziidae
Genus ***Trapezium*** Megerle v. Mühlfeld, 1811
Subgenus ***Neotrapezium*** Habe, 1951

Trapezium (***Neotrapezium***) ***ichinohense*** sp. nov.

Figures 4-1, 7a, b, 8a-c

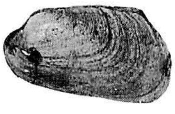
Type specimens.—IGPS Coll. Cat. No. 102605 (Holotype), No. 102606 (Paratypes).

Type locality.—Loc. 18; upper reaches of the Nesori River about 3 km east of Nosokei, Ichinohe town, Ninohe County, Iwate Prefecture.

Description.—Shell medium to large for the genus

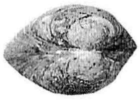
Figure 4. (All figures natural size).

1, 7a-b, 8a-c. *Trapezium* (*Neotrapezium*) *ichinohense* sp. nov., 1, 7a-b: Loc. 18, IGPS coll. cat. no. 102606, Paratypes, left valves, 8a-c: Loc. 18, IGPS coll. cat. no. 102605, Holotype, right valve. **2a-c, 3, 5a-c.** *Nipponomarcia nakamurai* (Ikebe), 2a-c, 5a-c: Loc. 15, IGPS coll. cat. no. 102600, 2a and 5b: right valves, 2a and 5c: left valves, 2c and 5a: apical view. 3: Loc. 3, IGPS coll. cat. no. 102598, left valve. **4, 6.** *Trapezium* (*Neotrapezium*) *modiolaeforme* Oyama and Saka, 4: Loc. 18, IGPS coll. cat. no. 102607, right valve, 6: Loc. 4, IGPS coll. cat. no. 102608, left valve. **9a-b, 10, 11.** *Dosinia* (*Phacosoma*) *kawagensis* Araki, 9a-b, 11: Loc. 10, IGPS coll. cat. no. 102590, 9a-b: right valve, 11: left valve, 10: Loc. 9, IGPS coll. cat. no. 102592, inner mould, right valve. **12.** *Crassostrea gigas* (Thunberg), Loc. 10, IGPS coll. cat. no. 102566, right valve.


1


2a


2b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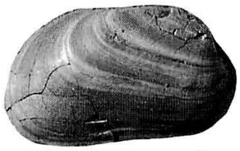
3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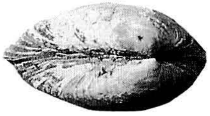
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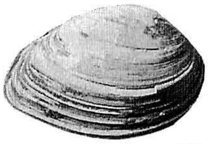
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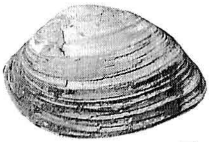
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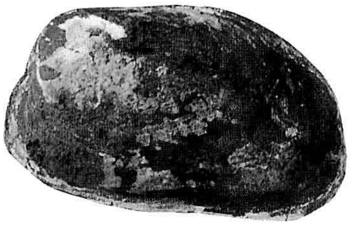
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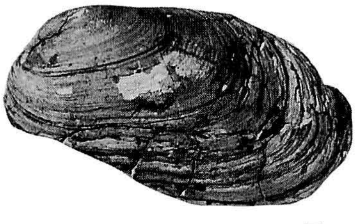
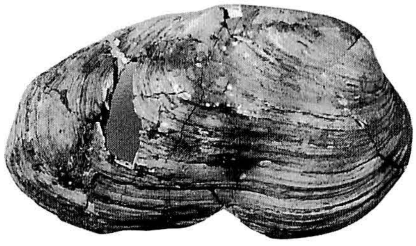

7a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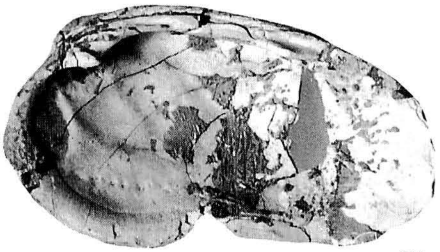
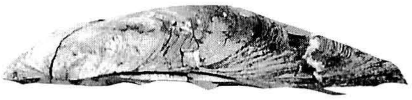

8b


7b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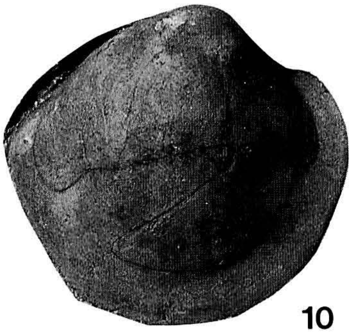
9a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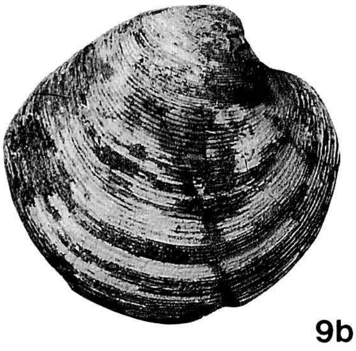
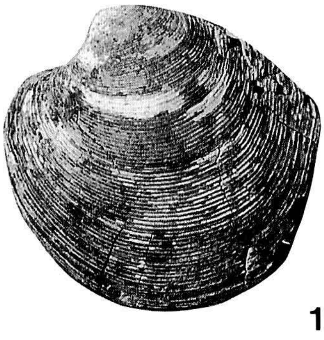
12


9b


11

Trapezium, elongate-trapezoidal in from, inequilateral, equivalve, thick, moderatey inflated; beak at about anterior one-ninth of shell length; anterior margin narrow, short, smoothly rounded; posterodorsal margin nearly straight in the young stages (shorter than about 30 mm), becoming gently curved downward with shell growth; posterior end of smaller specimens obliquely truncated, becoming rounded with growth; escutcheon narrow but distinct; shell surface undulates along concentrical growth lines that become lamella-like on escutcheon; blunt rounded ridge extends from beak to posteroventral margin, and ventromedial area of shell is broadly and shallowly depressed. Hinge area of right valve with single nodular cardinal tooth and a posterior lateral tooth; left valve has two stong teeth; pallial line and anterior adductor muscle scar distict and well impressed; posterior adductor muscle scar indistinct and ovate in form.

Remarks.—This species is characterized by its rather large size, thick shell, surface undulating along growth lines, obliquely truncated posterior end which becomes rounded with shell growth, and gently curved posterodorsal margin.

Comparison.—*Trapezium* (*Neotrapezium*) *liratum* Reeve, a Recent species, resembles *T.* (*N.*) *ichinohense*, but differs in having a smaller shell with a rather strong plate extending along the escutcheon. The new species differs from *T.* (*N.*) *isomatsuense*, originally described from the Isomatsu Formation in Aomori Prefecture by Kotaka (1955), in having a more elongate shell with a nearly straight posterodorsal margin and a narrower anterior area. *Trapezium* (*Neotrapezium*) *isoharense* Kamada, 1962, from the Kunugidaira Formation is distinguished from the present species by its smaller size, less rounded and shorter anterodorsal margin, and more strongly curved posterodorsal margin. *Trapezium* (*Neotrapezium*) *modiolaeforme* Oyama and Saka differs in having a thinner shell with a rather smooth suface and a less developed escutcheon. *T.* (*N.*) *ichinohense* is easily distinguished from *T.* (*N.*) *chonbugense* Yoon, 1976, by having a broader posterior area and curved posterodorsal margin.

Locality.—4, 10, 18 (No. 102605, 102606).

Measurements (*in mm*).—

IGPS Coll. Cat. No.	Length	Height	Depth	*Bp	Bp/Length	Valve
102605 (Holotype)	54.4	29.3	9.5	6.2	0.114	Right
102606-1 (Paratype)	45.8	24.7	8.1	5.7	0.124	Left
102606-2 (Paratype)	44.4	22.2	8.5	6.5	0.146	Right
102606-3 (Paratype)	22.6	12.0	3.5	2.4	0.106	Left
102606-4 (Paratype)	20.7	11.2	3.2	2.8	0.135	Right

*Beak position from anterior end.

Trapezium* (*Neotrapezium*) *modiolaeforme
Oyama and Saka, 1944

Figures 4-4, 6

Trapezium modiolaeformis Oyama and Saka, 1944, p. 141, pl. 15, figs. 12a, b, 13a, b; Itoigawa in Itoigawa *et al.*, 1974, p. 80, pl. 20, figs. 8, 9.

Trapezium modiolaeforme Oyama and Saka. Itoigawa and Nishikawa, 1976, pl. 33, fig. 10; Itoigawa *et al.*, 1981, 1982, p. 73, 74, pl. 13, figs. 11a, b; Shibata and Ina, 1983, p. 47, pl. 5, fig. 8; Shibata *et al.*, 1987, pl. 1, fig. 5; Iwamura Research Group, 1989, pl. 12, fig. 1; Okamoto *et al.*, 1990, pl. 9, fig. 4; Muramatsu, 1992, pl. 49, fig. 4.

Remarks.—*T.* (*N.*) *modiolaeforme* is characterized by its rather thin, high and moderately inflated shell, the surface of which is smooth in the younger stage and becomes sculptured with fine concentric growth lines with shell growth, and by its less well developed escutcheon.

Locality.—4 (No. 102608), 5, 9, 13, 18 (No. 102607).

Distibution.—? Furanui F. of Hokkaido (Uchimura and Majima, 1992), Neba F., and Arakida F. of the Tomikusa Gr. in Nagano Pref., Kawakado F. of the Shitara Gr. in Aichi Pref., Akeyo F. of the Mizunami Gr. in Gifu Pref., "lower sandstone formation" of the Bihoku Gr. in Hiroshima Pref.

Measurements (*in mm*).—

IGPS Coll. Cat. No.	Length	Height	Depth	*Bp	Bp/Length	Valve
102507-1	30.0	17.0	5.5	4.0	0.133	Right
102507-2	48.3	24.0+	—	—	—	Left
102507-3	34.8+	25.8+	9.1	—	—	Right

*Beak position from anterior end.

Family Veneridae
Genus **Dosinia** Scolpi, 1777
Subgenus **Phacosoma** Jukes-Brown, 1912

Dosinia* (*Phocosoma*) *kawagensis Araki, 1960

Figures 4-9a, b, 10, 11

Dosinia nomurai Otuka. Itoigawa, 1956, pl. 2, fig. 3. [not of Otuka, 1934]

Dosinia japonica kawagensis Araki, 1960, p. 95, pl. 7, fig. 3.

Dosinia (*Phacosoma*) *kawagensis* Araki. Masuda, 1963b, pl. 4, figs. 1-8; Yoon, 1979, p. 15, pls. 7, 9, 10.

Dosinorbis kawagensis (Araki). Itoigawa in Itoigawa, *et al.*, 1974, p. 87, 88, pl. 23, figs. 1a-6.

Phacosoma kawagensis (Araki). Itoigawa *et al.*, 1981, 1982, p. 80, 81, pl. 14, figs. 6a, b; Shibata and Ina, 1983, p. 48, pl. 5, fig. 12; Itoigawa and Shibata, 1986, pl. 16, fig. 13; Muramatsu, 1992, pl. 49, fig. 6.

? *Dosinia kawagensis* Araki. Hayashi and Miura, 1973, pl. 1, fig. 12.

Dosinia (*Phacosoma*) *nomurai* Otuka. Lee, 1992, p. 92, figs. 31-3, -9. [not of Otuka, 1934]

Dosinia anguloides Nomuma. Hata, 1967, pl. 4, figs. 2, 3. [not of Nomura, 1935d]

Remarks.—This species was originally described by

Araki (1960) from the Miocene Kaisekizan Formation of the Ichishi Group in Mie Prefecture as a subspecies of *D.* (*P.*) *japonica* Reeve, a living species, and was based on a single poorly preserved left valve. Subsequently, Masuda (1963b) redescribed it from well-preserved specimens from the Akeyo Formation of the Mizunami Group, from the Ajiri Formation of Miyagi Prefecture, and from the Shiote Formation of Fukushima Prefecture and raised it to specific rank. The species is characterized by its medium-sized, suborbicular and rather inflated shell with a rounded swollen beak area, upwardly curved anterior margin, sculpture of regular flat-topped concentric growth lines that become lamellate near the antero- and posterodorsal margins, and obliquely subtruncated posteroventral margin.

Comparion.—The living *Dosinia* (*Phacosoma*) *japonica* Reeve is similar to *D.* (*P.*) *kawagensis*, but is distinguished by having a less inflated shell with a less swollen beak area.

Dosinia anguloides Nomura, 1935, described from the Ajiri Formation in Miyagi Prefecture, is distinguished by its higher, less inflated shell with a more pointed beak.

Locality.—1, 2, 7, 9 (No. 102592), 10 No. 102590), 11, 18 (No. 102591).

Distribution.—Ajiri F. in Miyagi Pref., Shiote F. in Fukushima Pref., Kawakado, Shimoda and Kuroze Fs. of the Shitara Gr., and ? Okazaki F. in Aichi Pref., Tôyama and Akeyo Fs. of the Mizunami Gr. in Gifu Pref., Chikusa F., and Tsuchiyama and Kurokawa Fs. of the Ayugawa Gr. in Shiga Pref., Okuyamada F. of the Tsuzuki Gr. in Kyoto Pref., Nenobi Granule Conglomerate and Hiramatsu Sandstone and Siltstone Fs. of the Awa Gr., and Ôi and Katada Fs. of the Ichishi Gr. in Mie Pref., Japan. Sinhyeon Formation in the Ulsan district, Korea.

Measurements (*in mm*).—

IGPS Coll. Cat. No.	Length	Height	Thickness	*Bp	Bp/ Length	Valve
102590-1	45.2	42.8	12.4	14.5	0.321	Right
102590-2	42.8	40.3	11.0	11.2	0.262	Left
102590-3	45.8	40.0	12.4	14.0	0.306	Left
102590-4	48.9	45.2	15.5	15.8	0.323	Right
102590-5	25.1	24.4	6.3	7.0	0.279	Right
102591-1	41.4	41.4	11.0	11.7	0.283	Right
102591-2	36.7	34.6	9.0	10.2	0.278	Left
102591-3	29.3	27.1	7.5	7.5	0.256	Left
102592	45.5	41.0	13.9	13.9	0.305	Left

*Beak position from anterior end

Genus **Ruditapes** Chiamenti, 1900

Ruditapes miyamurensis (Itoigawa, 1956)

Figures 5-4, 5, 7, 10

Tapes (*Amygdala*) *miyamurensis* Itoigawa, 1956, p. 189, pl. 1, figs. 2, 3.

? *Ruditapes miyamurensis* (Itoigawa). Itoigawa in Itoigawa *et al.*, 1974, p. 89, pl. 25, figs. 9, 10a-b.

Ruditapes miyamurensis (Itoigawa). Itoigawa *et al.*, 1982, p. 83.

Description.—Shell of medium to large size, transversely elongate, with rounded subtrigonal outline in younger stages becoming subtrapezoidal with shell growth, inequilateral, equivalve, moderately inflated, moderately thick ; posterodorsal margin long ; anterior margin smoothly rounded, posterior margin gently rounded and subtruncated or subangular ; beak low, small, prosogyrate, situated at about anterior one-third of shell length ; lunule shallow, very small, elongate oblong in form, defined by fine furrow ; escutcheon narrow ; shell surface sculptured with many radial threads and concentric growth lines ; radial threads broader than their interspaces, much stronger than growth lines, and imbricated in latero-dorsal areas ; inner ventral margin smooth ; pallial sinus oblique linguiform, and up to three-sevenths of shell length in depth.

Comparison.—This species closely resembles *Ruditapes philippinarum* (Adams and Reeve), a living species, but is distinguished by its more strongly subtruncated posterior and greater number of radial threads. *Ruditapes takagii* (Masuda, 1956), originally described from the Higashi-innai Formation in Ishikawa Prefecture, differs in having a smaller shell with a more rounded posterior end and less promient umboal area.

Locality.—1, 2, 3, 4, 5 (No. 102601), 6, 7, 8a, 8b, 11 (No. 102602), 12, 13, 15, 18 (No. 102603).

Distribution.—Okuyamada F. of the Tsuzuki Gr. in Kyoto Prefecture, Akeyo F. of the Mizunami Gr. in Gifu Pref., Tsuchiyama and Kurokawa Fs. of the Ayugawa Gr. in Shiga Pref., Nenobi Granule Conglomerate and Hiramatsu Sandstone and Siltstone Fs. of the Awa Gr. (Shibata, 1978).

Measurements (*in mm*).—

IGPS Coll. Cat. No.	Length	Height	Depth	*Bp	Bp/ Length	Valve
102603-1	54.2	40.3	11.7	18.1	0.334	Right
102603-2	57.5+	40.4+	10.4	24.5	—	Left
102603-3	61.3	46.8	12.6	20.2	0.330	Right
102603-4	57.8+	40.8	11.5	19.8	—	Right
102603-5	61.8+	45.0+	12.7+	—	—	Left
102603-6	56.1+	42.2+	13.5+	—	—	Left
102603-7	52.1+	39.0	13.0	16.5	—	Left
102603-8	63.0+	ca. 43.1	12.2	22.8	—	Right
102603-9	21.5+	15.8	5.3	7.5	—	Left
102603-10	59.4	41.6	11.6	19.7	0.332	Left

*Beak position from anterior end.

Genus **Nipponomarcia** Ikebe, 1941

Nipponomarcia nakamurai (Ikebe, 1941)

Figures 4-2a-c, 3, 5a-c

Katelysia (*Nipponomarcia*) *nakamurai* Ikebe, 1941, p. 50-53, pl. 2, figs. 1-8.

Nipponomarcia nakamurai (Ikebe). Itoigawa, 1955a, p. 176-184 ; Itoigawa, 1955b, pl. 6, fig. 6 ; Itoigawa, 1956, pl. 1, fig. 4 ; Kamada, 1962, p. 118, pl. 13, figs. 10-12 ; Mizumo, 1964, p. 605, pl. 3, figs. 2-6 ; Uozumi and Fujie, 1966, p. 152, pl. 12, figs. 1, 2 ; Itoigawa in Itoigawa *et al.*, 1974, p. 88, 89, p.

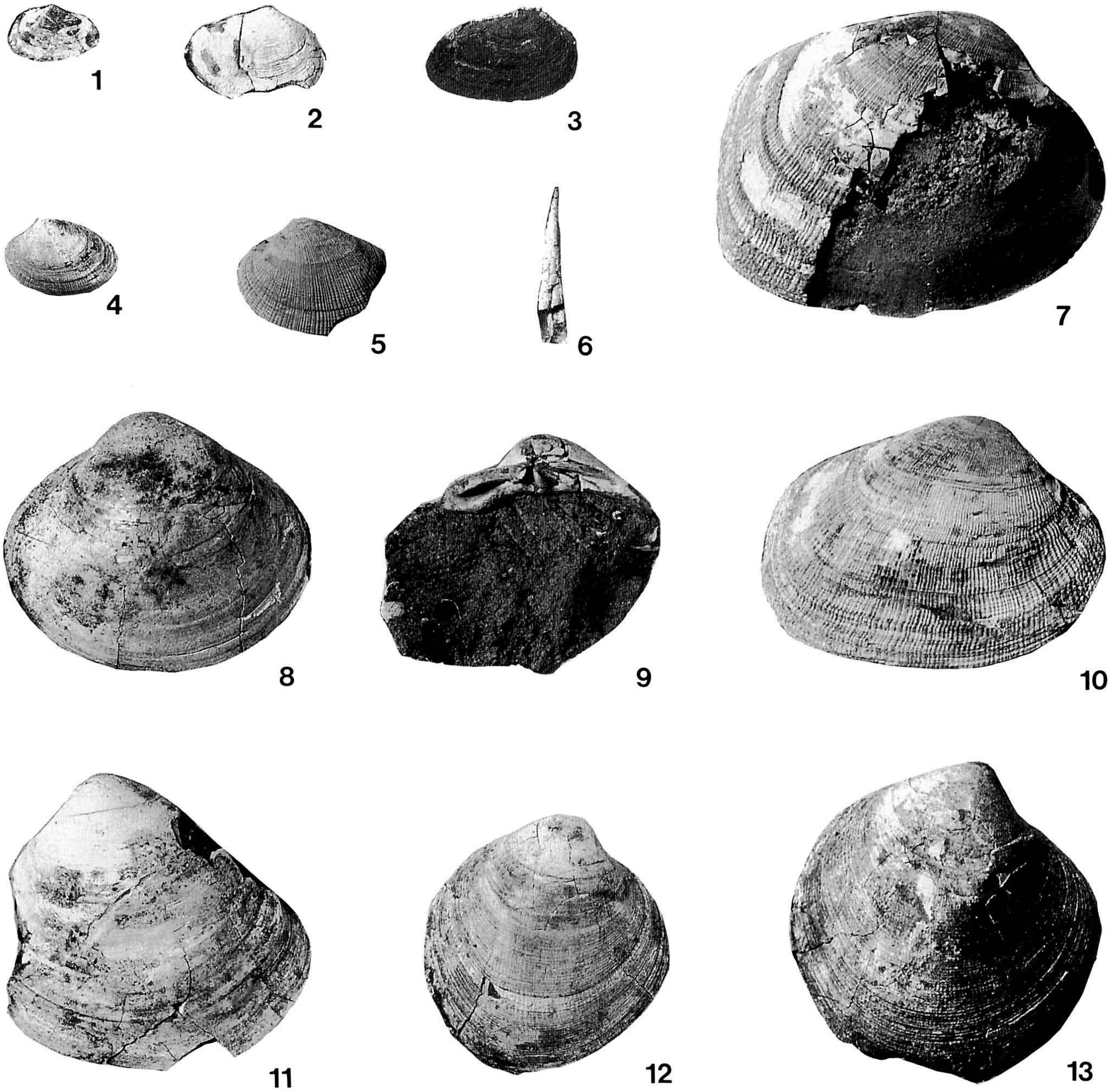


Figure 5. (All figures natural size unless otherwise stated).

1, 2, 3. *Mya* sp., 1, 2 : Loc. 19, IGPS coll. cat. no. 102609, 1 : left valve, 2 : right valve, 3 : Loc. 17, IGPS coll. cat. no. 102611, right valve. **4, 5, 7, 10**. *Ruditapes miyamurensis* (Itoigawa), 4 : Loc. 11, IGPS coll. cat. no. 102602, left valve, 5, 7, 10 : Loc. 18, IGPS coll. cat. no. 102603, 5 : right valve, 7, 10 : right valve. **6**. *Laevidentalium* ? sp., Loc. 19, IGPS coll. cat. no. 102637, ×1.5. **8, 9, 11**. *Meretrix arugai* Otuka, Loc. 10, IGPS coll. cat. no. 102604, 8, 11 : left valves, 9 : right valve (showing cardinal teeth). **12, 13**. *Cyclina japonica* Kamada, Loc. 10, IGPS coll. cat. no. 102649, right valves.

25, figs. 5a-6b ; Itoigawa *et al.*, 1981, 1982, p. 86, 87, pl. 16, figs. 1a, b ; Itoigawa and Shibata, 1986, pl. 16, fig. 10 ; Shibata *et al.*, 1987, pl. 1, fig. 8 ; Kanno *et al.*, 1988, p. 380, 381, pl. 1, fig. 11 ; Okamoto *et al.*, 1989, pl. 6, figs. 13-15 ; Okamoto *et al.*, 1990, pl. 9, fig. 23 ; Muramatsu, 1992, pl. 49, fig. 7.

? *Caryocorbula saikawai* Kotaka, 1955, p. 27, 28, pl. 2, figs. 5, 6.

Nipponomarkia nakamurai (Ikebe). Hayashi and Miura, 1973, pl. 1, fig. 8 (misspelling of *Nipponomarcia*).

?*Nipponomarcia "nakamurai"* (Ikebe). Taguchi *et al.*, 1979, pl. 2, fig. 16.

not *Nipponomarcia nakamurai* (Ikebe). Nakagawa and Takeyama, 1985, p. 16, fig. 4 ; Ozawa *et al.*, 1986, pl. 14, fig. 7. [*Nipponomarcia imobarensis* Itoigawa and Nishikawa, 1976]

Remarks.—*Nipponomarcia nakamurai* from the Yotsuyaku Formation is characterized by a small, well inflated, subtrigonal shell with a rounded ridge extending from the beak to the posteroventral margin. In young stages, the shell surface is nearly smooth, with a small lunule defined by a distinct fine line, thereafter fine growth lines become distinct and irregular and the lunule becomes indistinct with shell growth. *Caryocorbula saikawai*, originally described by Kotaka (1955) from the Isomatsu Formation, Aomori Prefecture, based on a single right valve, is considered from its shell morphology to be a synonym of the present species.

Nipponomarcia nakamurai, figured by Nakagawa and Takeyama (1985) and Ozawa *et al.* (1986) from the Shimo Formation of the Uchiura Group in Fukui Prefecture, is not this species, but *Nipponomarcia imobarensis* Itoigawa and Nishikawa, 1976, from the radial threads on the posterodorsal area of the shell.

Locality.—1, 2, 3 (No. 102598), 4, 5, 6 (No. 102597), 7, 8a, 10, 11, 12, 13 (No. 102599), 15 (No. 102600), 16.

Distribution.—Tsurikake and Kunnui Fs. of Hokkaido, Isomatsu F. in Aomori Pref., Kunugidaira F. of the Yunagaya Gr. in Fukushima Pref., Okazaki F. in Aichi Pref., Neba F. in Nagano Pref., Tôyama and Akeyo Fs. of the Mizunami Gr. in Gifu Pref., Tsuchiyama and Kurokawa Fs. of the Ayugawa Gr. in Shiga Pref., Nenobi Granule Conglomerate F. of the Awa Gr. in Mie Pref., Okuyamada and Yuantani F. of the Tsuzuki Gr. in Kyoto Pref., "lower sandstone formation" of the Bihoku Gr. in Hiroshima Pref.

Measurements (*in mm*).—

IGPS Coll. Cat. No.	Length	Height	*Depth	Valve
102600-1	26.8	18.4	14.4	Both
102600-2	17.9	12.1	12.0	Both
102600-3	26.0	21.2	16.9	Both
102600-4	23.2	17.0	12.5	Both
102600-5	26.0	18.0	13.3	Both
102600-6	20.0	15.4	11.3	Both
102600-7	28.1	21.1	17.8	Both
102600-8	18.6	13.6	10.3	Both
102600-9	27.0	20.9	15.1	Both
102600-10	21.8	15.9	12.3	Both
102600-11	24.7	18.0	13.7	Both
102600-12	21.6	14.8	11.0	Both

*Both valves

Genus **Meretrix** Lamarck, 1799

Meretrix arugai Otuka, 1938

Figures 5-8, 9, 11

Meretrix arugai Otuka, 1938, p. 30, 31, figs. 11, 12 ; Hatai, 1940, p. 129 ; Araki, 1960, p. 93, 94, pl. 7, fig. 5 ; Itoigawa in Itoigawa *et al.*, 1974, p. 86, pl. 22, figs. 5a-8 ; Itoigawa and Nishikawa, 1976, pl. 34, fig. 31 ; Taguchi *et al.*, 1979, pl. 3, fig. 8 ; Itoigawa *et al.*, 1981, 1982, p. 89, pl. 17, figs. 4a, b, 5a, b ; Takahashi, 1984, pl. 1, fig. 2 ; Itoigawa and Shibata, 1986, pl. 17, fig. 5 ; Sasaki and Ogasawara, 1986, pl. 5, figs. 7a, b ; Nakagawa, 1989, pl. 1, fig. 8 ; Okamoto *et al.*, 1989, pl. 6, fig. 12 ; Noda *et al.*, 1989, pl. 25, figs. 5a, b ; Noda *et al.*, 1994, figs. 6, 10, -14a, b, -18.

? *Meretrix arugai* Otuka. Ogasawara and Noda, 1978, p. 35-37, pl. 3, figs. 17, 20, 22a, b. [? *Meretrix ninohensis* Hatai]

not *Meretrix arugai* Otuka. Hatai, 1940, p. 129. [*Meretrix ninohensis* Hatai]

not *Meretrix arugai* Otuka. Ogasawara *et al.* eds., 1986, pl. 1, fig. 20 [*Meretrix ninohensis* Hatai]

Remarks.—Hatai (1940) described *Meretrix meretrix ninohensis* from the latest Early-early Middle Miocene Kadonosawa Formation of Iwate Prefecture, noting that *M. meretrix ninohensis* is distinguished from *M. arugai* by possessing a less produced and rounded beak area and less well differentiated anterior and posterior margins. Subsequently, Ogasawara and Noda (1978) claimed that these two species are conspecific as a result of measurements of height and length. Using only these two parameters, it is difficult to establish morphological differences between the Recent species. Based on comparison between *M. ninohensis* (topotype specimens) and *M. arugai* from the Kadonosawa Formation by the writer, it is considered that the two species are not conspecific because *M. ninohensis* has a distinctly more rounded and blunter beak area than *M. arugai*, as noted by Hatai (1940). Specimens from the Yotsuyaku Formation have a rather narrow beak area and are therefore referable to *M. arugai* Otuka.

Locality.—10 (No. 102604).

Distribution.—Kadonosawa F. in Iwate Pref., ? Tsukinoki F. in Miyagi Pref., Kunugidaira F. of the Yunagaya Gr. and Nakayama F. in Fukushima Pref., Tamagawa F. in Ibaraki Pref., Sunakozaka F. in Ishikawa Pref., Akeyo F. of the Mizunami Gr. in Gifu Pref., Kunimi F. in Fukui Pref., Bihoku Gr. in Hiroshima and Okayama Prefs.

Measurements (*in mm*).—

IGPS Coll. Cat. No.	Length	Height	Depth	Valve
102604-1	48.8	38.7	13.8	Left
102604-2	47.8+	45.1	13.3	Left
102604-3	52.8+	51.7	16.8	Right
102604-4	45.1+	34.2+	17.7	Right

Genus **Cyclina** Deshayes, 1850

Cyclina japonica Kamada, 1952

Figures 5-12, 13

Cyclina chinensis (Chemnitz). Yokoyama, 1926a, p. 222, pl. 28.

Cyclina sinensis (Gmelin). Otuka, 1934, p. 168; Makiyama, 1958, pl. 39, fig. 7.

Cyclina (*Cyclina*) *japonica* Kamada, 1952, p. 168, 169, pl. 15, figs. 1a, b, 2; Kamada, 1962, p. 115, pl. 13, fig. 4; Kim *et al.*, 1974, p. 277, pl. 38, fig. 9; Itoigawa in Itoigawa *et al.*, 1974, p. 88, pl. 25, figs. 11a, b, 12a-c; Ogasawara and Noda, 1978, p. 32, pl. 3, figs. 6, 13, 18, 21a, b; Itoigawa *et al.*, 1981, 1982, p. 90, 91, pl. 17, figs. 7a, b; Noda *et al.*, 1989, pl. 25, figs. 6a, b, 12; Lee, 1992, p. 95, figs. 32-7-9; Muramatsu, 1992, pl. 49, fig. 8.

? *Cyclina mitsuchii* Oyama (MS). Ogasawara and Tanai, 1952, p. 208, pl. 19, figs. 6a, b, 7. [*nomen nudum*]

Cyclina japonica Kamada. Kaseno, 1956, p. 6, pl. 2, figs. 8a-d; Iwai, 1965, p. 41, 42, pl. 12, figs. 3, 4; Shibata and Ina, 1983, p. 50, pl. 6, fig. 1; Itoigawa and Shibata, 1986, pl. 16, fig. 7; Nakagawa, 1989, pl. 1, figs. 4a-c; Kobayashi and Ueda, 1991, p. 135, 136, pl. 1, figs. 4, 5; Suzuki *et al.*, 1994, pl. 49, fig. 8.

Cyclina (s.s.) *japonica* Kamada. Tanaka, 1961, p. 76, pl. 1, figs. 39, 40; Yoon, 1976a, p. 15, pl. 1, figs. 15, 16; Yoon, 1979, p. 17, pl. 1, fig. 14.

? *Cyclina japonica* Kamada. Nakagawa and Takeyama, 1985, pl. 18, figs. 4a-c; Ozawa *et al.*, 1986, pl. 14, fig. 5. [? *Cyclina lunulata* Makiyama, 1926]

Remarks.—This species was originally described from the lower Middle Miocene Higashi-innai Formation in Ishikawa Prefecture, characterized by its slightly higher than long, rather inequilateral, well inflated and subtrigonal or suborbicular shell with surface sculpture of numerous fine, distinct concentric growth lines and radial striae, and by its rather produced anterior margin and subtruncated posterior margin.

Ogasawara and Tanai (1952) discussed and figured *Cyclina mitsuchii* Oyama (MS) from the lower Middle Miocene Oyama Formation in Yamagata Prefecture without designation of a holotype specimen or type locality, but the species was neither described nor figured by Dr. K. Oyama subsequently. Consequently, the present writer regards this species as a *nomen nudum.* In addition, judging from the morphological characters of the species as reported by Ogasawara and Tanai (1952), *C. mitsuchii* is a synonym of *C. japonica.*

Comparison.—*Cyclina sinensis* (Gmelin), a living species, closely resembles *C. japonica*, but is distinguished by possessing a more strongly incurved and elevated umbonal area. *Cyclina takayamai*, named by Oyama (1950) for *Cyclina sinensis* (Gmelin) of Otuka (1938) from the Bihoku Group in Okayama Prefecture, is distinguished by its more circular, equilateral and smaller sized shell, as pointed out by Kamada (1952). The present species rather resembles *Cyclina lunulata* Makiyama, which however possesses stronger concentric growth lines and more weakly developed radial striations than *C. japonica* and has partly crenulated inner ventral margin. *Cyclina "hwabongiensis"* Yoon and Noda, 1978, may be distinguished from the present species by possessing stronger radial threads only on the anterior half of the shell. In addition to these, one should consider *Cyclina yatsuoensis* Tsuda, 1959, and *C. kamadae* Araki, 1959, which have been described from upper Lower-lower Miocene strata. Specimens of the genus *Cyclina* are easily deformed even if the shell material is completely preserved, and the synonymy between these and *C. japonica* must be examined.

Locality.—8b (No. 102593), 10, (No. 102594).

Distribution.—Takinoue and Kunnui Fs. of Hokkaido, Kadonosawa F. in Iwate Pref., Sugota F. in Akita Pref., Ajiri and Tsukinoki Fs. in Miyagi Pref., Oyama F. in Yamagata Pref., Shiote F., Kunugidaira F. of the Yunagaya Gr. and Nakayama F. in Fukushima Pref., Asagawa F. in Ibaraki Pref., Tsugawa and Orito Fs. in Niigata Pref., Kurosedani F. in Toyama Pref., Sunakozaka and Higashiinnai Fs. in Ishikawa Pref., Moriya F., and Ôshimojo and Arakida Fs. of the Tomikusa Gr. in Nagano Pref., Kawakado F. of the Shitara Gr. in Aichi Pref., Tôyama and Akeyo Fs. of the Mizunami Gr. in Gifu Pref., Okuyamada F. of the Tsuzuki Gr. in Kyoto Pref., Tsuchiyama and Kurokawa Fs. of the Ayugawa Gr. in Shiga Pref., Ôi F. of the Ichishi Gr. in Mie Pref., Kunimi F., and Shimo F. of the Uchiura Gr. in Fukui Pref., Japan. Cheongogsa F. in the Pohang district, Sinhyeon F. in the Ulsan district and Songjeon F. in the Eoil district, Korea.

**Measurements* (*in mm*).—

IGPS Coll. Cat. No.	Length	Height	Depth	Valve
102594-1	49.4	49.5	ca. 27.4	both
102495-2	39.9	40.9	22.1	both
102495-3	46.0	45.5	ca. 27.7	both
102594-4	42.8	48.5	ca. 27.3	both

*All specimens are slightly deformed.

Family Myidae

Genus **Mya** Linnaeus, 1758

Mya sp. indet.

Figures 5-1—3

Remarks.—Several imperfect specimens have been collected. The species is characterized by its small size, transversely elongate shell with rounded anterior and roundly subtruncated posterior margins, and the shell surface being sculptured with fine, low concentric growth threads. Although its hinge area can not be examined, the species is referable to the genus *Mya*, on the basis of the shell features and morphology of the pallial sinus.

Locality.—14a, 14b, 17 (No. 102611), 19 (No. 102609).

Class Scaphopoda
Order Dentaloida
Family Laevidentaliidae
Genus ***Laevidentalium*** Cossmann, 1888

Laevidentalium ? sp. indet.

Figure 5-6

Remarks.—Many compressed specimens have been obtained. They show the following morphologic features ; shell small in size, slender, dentaloidal in form and weakly curved dorsally ; circular in section ; surface smooth ; apex truncated ; apical notch not observed. These features show the specimens to be referable to the genus *Laevidentalium* provisionally.

Locality.—19 (No. 102637).

References cited

Full references are to be presented in the following Part 2 (2).

Erratum

The typification of specimen described in the Ohana and Kimura paper (Transactions and Proceedings of the Palaeontological Society of Japan, N.S., No. 178, p. 140, line 25) is given incorrectly as the lectotype. The specimen should have been disignated as the hypotype.

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