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Analysis of Ammonoid Assemblages in the Upper Turonian of the Manji Area, Central Hokkaido

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Introduction

The analysis of actual assemblages is as much an important approach as functional morphologic examination at individual level for the reconstruction of ammonoid habitats. It has already been realized empirically that ammonoids are one of the most important biofacies indicators to estimate paleoenvironments and paleogeography (WESTERMANN, 1954; MATSUMOTO, 1965a, 1971; KAUFFMAN, 1967; HALLAM, 1969, 1971; WENDT, 1971; MATSUMOTO and OKADA, 1973; KENNEDY and COBBAN, 1976; WIEDMANN, 1976; OBATA and FUTAKAMI, 1977).

However, quantitative study of ammonoid assemblages has not yet been satisfactorily attempted since SCOTT's (1940) pioneer work.

The ammonoids in the Upper Cretaceous of the meridional zone of Hokkaido may be suitable material for the assemblage paleoecologic study, because they occur abundantly throughout the sequences in various areas in a good state of preservation. Moreover, as a result of studies on sedimentary facies (TANAKA, 1963, 1970), paleocurrent directions (TANAKA, 1970; TANAKA and SUMI, 1975), and petrography of clastic sediments (MATSUMOTO and OKADA, 1971), it has become made clear that the lateral changes in sedimentary facies from inshore shallow water facies to offshore flysch facies can be recognized continuously from west to east in the Upper Cretaceous of the central zone of Hokkaido. We can, therefore, examine the lateral changes in ammonoid assemblages with sedimentary facies. The lateral changes in litho- and ammonoid facies are particularly conspicuous in the Turonian (MATSUMOTO and OKADA, 1973; TANABE, *in press*). Accordingly we select the Turonian ammonoid assemblages of Hokkaido as the basis of the present study.

Although TANABE (*in press*) has already studied the Middle Turonian ammonoid assemblages in the intermediate facies (=*Scaphites* facies) between the nearshore and offshore facies in the Saku, Obira and Oyubari areas, further works on the ammonoid assemblages in the nearshore and offshore facies of the Turonian are needed to determine the relationship between morphotypes and lithofacies.

This paper presents the results of assemblage analysis on the 26 ammonoid samples comprising 2,195 individuals of 24 species from the Upper Turonian shallow water facies of the Manji area, western central part of the meridional zone of Hokkaido. The species composition and species diversity in several samples from the Upper Turonian intermediate facies of the Saku, Obira and Oyubari areas are briefly described in comparison with those of the Manji area. The problem of post-mortem transportation in the formation of fossil ammonoid assemblages and presumable habitats of the Turonian ammonoids in Hokkaido are discussed in this paper on the basis of the obtained data and the selected previous works.

Material

Note on the litho- and biofacies of the Upper Turonian in the Manji area.——The marine fossiliferous Cretaceous deposits are narrowly crop out in the Manji area, central Hokkaido, forming a gentle dome structure called the Manji dome. The Cretaceous sequences in this area together with those in the adjacent Yubari and Pombets areas are geologically important, because they represent the observable westernmost facies of the marine fossiliferous deposits of the Cretaceous basin of Hokkaido (Yezo geosyncline). The Cenomanian and the Turonian in this area consist of much coarser clastic sediments than those in the eastern and central parts of the geosyncline; hence, they have been defined as a local lithostratigraphic unit, Mikasa Formation.

OBATA and FUTAKAMI (1975, 1977) have recently described the stratigraphy of the Cretaceous in this area. Based on these works, a geologic map in the northern part of the Manji dome and stratigraphic columnar sections along the selected routes are shown in Figs. 1–2 respectively.

The Turonian in this area is divided into two members, MK_2 (middle part of the Mikasa Formation) and MK_3 (upper part of the Mikasa). MK_2, more than 230 m thick, is characterized by fine- to coarse-grained massive sandstone with some intercalated beds of conglomerate. MK_3 attains about 120 m in maximum thickness, consisting mainly of fine-grained sandstone and silty sandstone. Several lenses of conglomerate are intercalated in the lower to middle parts of MK_3 in the western part of this area. Some beds with many ostreids, trigonians and other thick-shelled bivalves, and gastropods are contained at several horizons in the Turonian, especially in the Middle Turonian. Calcareous sandy nodules including numerous ammonoids, together with drifted plant remains and amber fragments are frequently found in the Upper Turonian.

From these lines of evidence, OBATA and FUTAKAMI (1975, 1977) concluded that

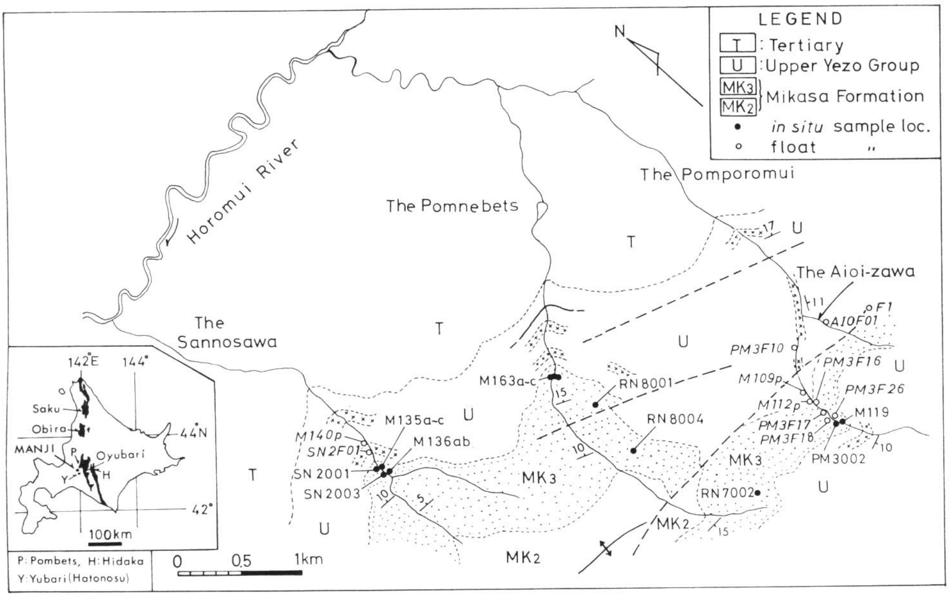


Fig. 1. Geologic map of the northern part of the Manji area, central Hokkaido (adapted from OBATA and FUTAKAMI, 1975) and the locations of ammonoid samples examined.

the Turonian in the Manji area had been deposited under the relatively inshore to nearshore shallow water environment.

Samples.——26 ammonoid samples comprising 2,195 individuals of 24 species from the Manji area have been studied on this occasion. Each sample, represented by more than 10 individuals, was carefully separated from a single calcareous nodule. The localities of these samples are shown in Fig. 1. Among the 26 samples examined, 15 samples with Roman locality number in Fig. 1, were obtained from calcareous nodules embedded in the upper part of member MK_3 (*see* Fig. 2). The remaining 11 samples, written by Italic locality number in Fig. 1, were collected from floated or fallen nodules in the streams of the Sannosawa, Pomporomui and Aioi-zawa, tributaries of the Horomui River. As fossiliferous nodules predominantly occur in the upper part of member MK_3 (*see* Fig. 2), most of the floated and fallen samples may have been derived from nearly the same stratigraphic level as *in situ* samples.

According to OBATA and FUTAKAMI (1975, 1977), the upper part of member MK_3 belongs to the upper part of *Inoceramus teshioensis* Zone (approximately Upper Turonian by MATSUMOTO's (1977) zonal scheme of the Upper Cretaceous in Japan). Indeed, every sample, regardless of *in situ* or fallen or floated condition, contains several specimens of *I. teshioensis*.

Repository.——Among the 26 samples examined, 12 samples with the prefix M were collected by K. TANABE and Y. MIYATA in 1977, and are stored in the type collection of Kyushu University. The remaining 14 samples were collected by I. OBATA

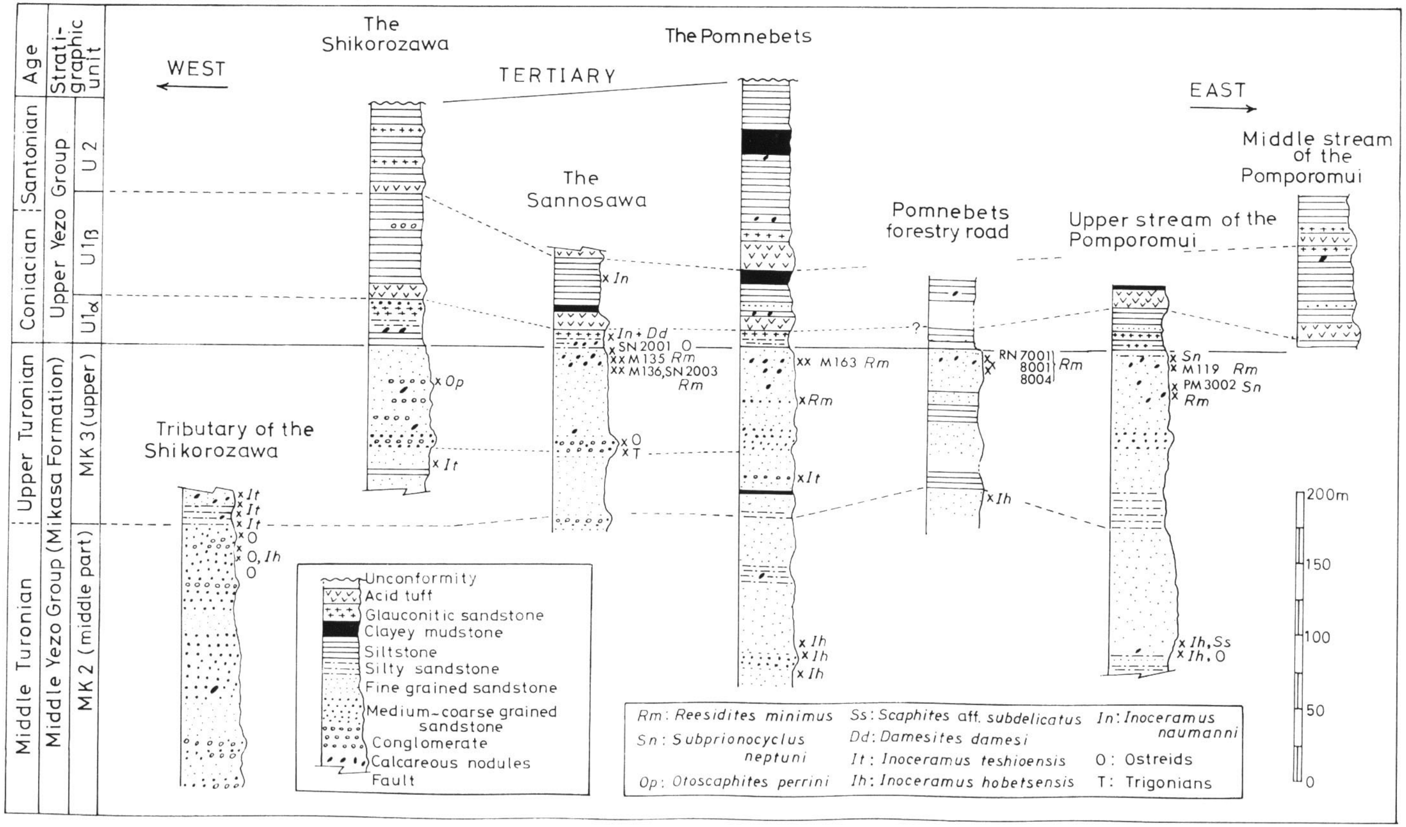


Fig. 2. Stratigraphic columnar sections of the post-Middle Turonian Cretaceous deposits along the selected routes in the Manji area, in which horizons of the examined ammonoid samples and important mega-fossils are indicated. Basic stratigraphic data are adapted from OBATA and FUTAKAMI (1975).

and M. FUTAKAMI in 1974 and 1975, and are stored in the type collection of the National Science Museum, Tokyo.

Analysis of Upper Turonian Ammonoid Assemblages

Species composition and diversity in samples.——The species composition and frequency of occurrence of the 24 species in the 26 samples examined are summarized in Table 1.

Reesidites minimus (HAYASAKA and FUKADA) and *Subprionocyclus neptuni*(GEINITZ), both belonging to the Collignoniceratidae, are the most dominant species in the Upper Turonian ammonoid fauna of the Manji area. The majority of the total number of specimens in every sample, except for SN 2001, is represented by *R. minimus* or *S. neptuni.* SN 2001 is composed of smooth or weakly ornate morphotype ammonites such as the desmoceratids and tetragonitids, and heteromorphs.

The frequency of occurrence of *R. minimus* is especially conspicuous in the 8 samples, M 135a–b, SN 2003, M 140p and SN 2F01 from the Sannosawa, M 119 from the Pomporomui, and in RN 8001 and RN 8004 from the exposures along the Pomnebets forestry road.

S. neptuni is restrictedly found in the eastern part of the northern Manji dome (Pomporomui and Aioi-zawa), and never occur sympatrically with *R. minimus.* Two heteromorph species, *Sciponoceras intermedium* MATSUMOTO and OBATA, and *Madagascarites ryu* MATSUMOTO and MURAMOTO also reach about 10% in the frequency of occurrence in certain samples. As compared with the above-mentioned 4 species, the frequency is generally low for any of the remaining 20 species, so far as the examined samples concerned.

In the next, the species diversity in each samples was examined by means of SIMPSON's (1949) index of concentration. The results are shown at the bottom of Table 1. Every sample except for SN 2001 has an index of concentration of more than 0.6; therefore the Upper Turonian ammonoid assemblages in the Manji area have a relatively simple species composition. SN 2001 is distinguished from the other samples for its large species diversity. Every sample, exclusive of SN 2001, from the Sannosawa has an extremely large SIMPSON's index of more than 0.95.

Comparison of species composition between a sample pair.——To compare the species composition between a sample pair quantitatively, KIMOTO's (1967) similarity index for species composition has been applied to the selected 18 samples of more than 20 individuals. The results are given in Table 2.

According to KIMOTO (1967, 1976), the similarity index ($C\pi$) ranges from zero to one, and if two samples are quite identical in respect of species composition, $C\pi$ is equal to one. High similarity is recognized in each pair among the *R. minimus*-bearing 14 samples (M 135a–c, M 140p, SN 2003, M 163a, c, SN 2F01, M 136a–b, RN 8001, RN 8004, M 119, PM 3F10) and also in each pair among *S. neptuni*-bearing 3 samples (M 112p, PM 3002, F1). KIMOTO's similarity index is, however, extremely

Table 1. Species composition and SIMPSON's (1949) index of concentration in the 26 ammonoid samples from the Upper Turonian of the Manji area.

Locality(=sample) number	Sannosawa									Pomnebets			Pomnebets road			Pomporomui									Aioizawa		Total number of each species
Species	M135a	M135b	M135c	M136a	M136b	SN2001	SN2003	*M140p*	*SN2F01*	M163a	M163b	M163c	RN8001	RN8004	RN7002	M 119	*PM3F10*	PM3002	*PM3F26*	*M112p*	*PM3F17*	*PM3F16*	*M109p*	*PM3F18*	*F 1*	*AIOF01*	
Neophylloceras subramosum Spath		1																									1
Phyllopachyceras ezoense (Yokoyama)						1																					1
Damesites ainuanus Matsumoto						7																					7
Tragodesmoceroides subcostatus Matsumoto						3			2						1												6
T. (?) sp.						2																					2
Yokoyamaoceras minimum Matsumoto						2																					2
Y. ornatum Matsumoto																						1			1		2
Mesopuzosia sp.						1																	1	1			3
Subprionocyclus neptuni (Geinitz)																		97	34	30	13	15	18	11	28		246
Reesidites minimus (Hayasaka & Fukada)	412	226	48	75	79		94	262	117	38	14	21	175	81	8	151	29									11	1841
Tetragonites glabrus (Jimbo)						2		1								1											4
Gaudryceras denseplicatum (Jimbo)						1				1			1						1		1						5
G. aff. *denseplicatum* (Jimbo)						1																					1
Anagaudryceras limatum (Yabe)																					1						1
A. sp.						1							1														2
Eubostrychoceras cf. *woodsi* (Kitchin)						1																					1
E. sp.						3																1					4
Madagascarites ryu Matsumoto & Muramoto													2					11									13
Nipponites (?) sp.									1																		1
Scalarites cf. *mihoensis* (Wright & Matsumoto)													1									1					2
S. sp.								2		1			2		1		1	1		1				1	1		11
Scaphites aff. *subdelicatus* Cobban & Gryc																						1					1
Otoscaphites perrini (Anderson)								1		2															1		4
Sciponoceras intermedium Matsumoto & Obata	1	1		1	1					6	1	3		1		14	3								1	1	34
Number of specimens in each sample	413	228	48	76	80	25	94	266	120	48	15	24	182	82	10	166	33	109	35	31	15	19	19	13	32	12	2195
Simpson's (1949) index of concentration	.99	.98	1.0	.97	.98	.10	1.0	.97	.95	.64	.87	.77	.92	.98	.78	.83	.78	.80	.94	.94	.74	.61	.90	.71	.76	.83	—

Table 2. Comparison of species composition between a sample pair among the selected 18 ammonoid samples from the Upper Turonian of the Manji area by means of KIMOTO's (1967) similarity index.

← West

Sample size N≧30

+ *Reesidites minimus*-bearing sample

++ *Subprionocyclus neptuni*-bearing sample

M135a+																	
M135b+	1.00																
M135c+	1.00	1.00															
M140p+	1.00	1.00	1.00														
SN2F01+	1.00	1.00	1.00	1.00													
M136a+	1.00	1.00	1.00	1.00	1.00												
M136b+	1.00	1.00	1.00	1.00	1.00	1.00											
SN2001	0	0	0	0	0	0	0										
SN2003+	1.00	1.00	1.00	1.00	1.00	1.00	1.00	0									
M163a+	.96	.96	.96	.97	.97	.97	.82	0	.96								
M163c+	.98	.98	.98	.98	.99	.99	.99	0	.98	.99							
RN8001+	1.00	1.00	1.00	1.00	.95	.95	1.00	0	1.00	.97	.99						
RN8004+	1.00	1.00	1.00	1.00	1.00	1.00	1.00	0	1.00	.97	.99	1.00					
M119+	.99	.99	.99	.99	.99	.99	.99	0	.99	.99	1.00	.99	.99				
PM3F10+	.99	.99	.99	.99	.99	.99	.99	0	.99	.99	1.00	.99	.99	1.00			
PM3002++	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0		
M112p++	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	.99	
F1++	0	0	0	0	0	0	0	0	0	.001	.001	0	0	.003	.003	.99	.99

East →

Table 3. KIMOTO's (1967) index for the degree of interspecific overlap in occurrence among the selected 16 ammonoid species constituting the 26 samples from the Upper Turonian of the Manji area.

Strongly ornate type	*R. minimus*															
	S. neptuni	0														
Heteromorphic type	*S. intermedium*	0.35	0.02													
	S. aff. *subdelicatus*	0	0.10	0												
	O. perrini	0.19	0.10	0.32	0											
	M. ryu	0.02	0.70	0	0	0										
	Eubostrychoceras sp.	0	0.03	0	0.27	0	0									
	Scalarites sp.	0.39	0.38	0.11	0	0.49	0.26	0								
Smooth or weakly ornate type	*G. denseplicatum*	0.15	0.18	0.17	0	0.35	0.00	0.29	0.35							
	T. glabrus	0.23	0	0.35	0	0	0	0.62	0.19	0.35						
	D. ainuanus	0	0	0	0	0	0	0.82	0	0.33	0.73					
	T. subcostatus	0.04	0	0	0	0	0	0.61	0.06	0.34	0.66	0.72				
	Mesopuzosia sp.	0	0.14	0	0	0	0	0.29	0.14	0.25	0.47	0.50	0.46			
	N. subramosum	0.22	0	0.05	0	0	0	0	0	0	0	0	0	0		
	Y. minimum	0	0	0	0	0	0	0.82	0	0.33	0.73	1.00	0.72	0.50	0	
	Y. ornatum	0	0.24	0.04	0.67	0	0	0	0.16	0	0	0	0	0	0	0

small in each pair between *R. minimus*-bearing and *S. neptuni*-bearing samples. SN 2001 has no similarity with other samples.

Interspecific overlap among the samples examined.——The interspecific overlap in occurrence among the selected 16 species in the examined samples was investigated with an aid of KIMOTO's (1967) index for degree of interspecific overlap. The results are summarized in Table 3. The degrees of overlap with other species in *R. minimus* and *S. neptuni* are generally small, exclusive of the case between *S. neptuni* and *M. ryu*. Among the heteromorphic ammonoids, such species as *S. intermedium, Scaphites* aff. *subdelicatus* COBBAN and GRYC, and *Otoscaphites perrini* (ANDERSON) also show small degrees of overlap with other species.

In contrast, degree of interspecific overlap occasionally indicates a large value among the smooth or weakly ornate type ammonites and a heteromorph species, *Scalarites* sp.

Mode of Occurrence of *R. minimus* and *S. neptuni*

As previously stated, both *R. minimus* and *S. neptuni* are the dominant species generally at different levels in the Upper Turonian ammonoid assemblages of the

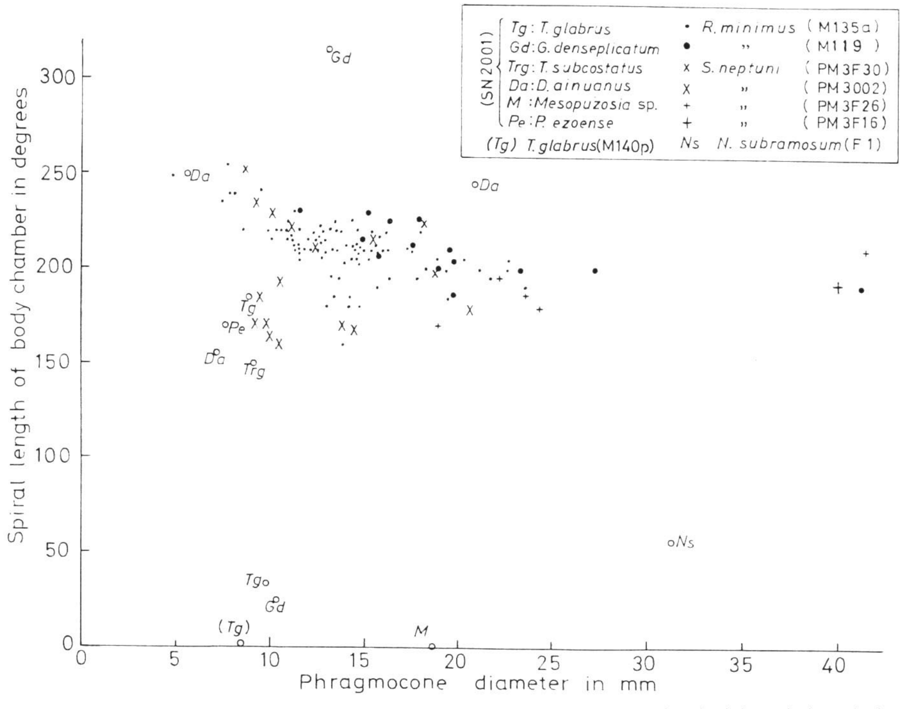


Fig. 3. Preservation rates of body chamber expressed by degrees of spiral length in relation to phragmocone diameter in some species among the selected 9 ammonoid samples from the Upper Turonian of the Manji area.

Manji area.

As TANABE (*in press*) pointed out, the concrete data on shell breakage, frequency of presence of aptychi or anaptychi, and size-frequency distribution of a species as

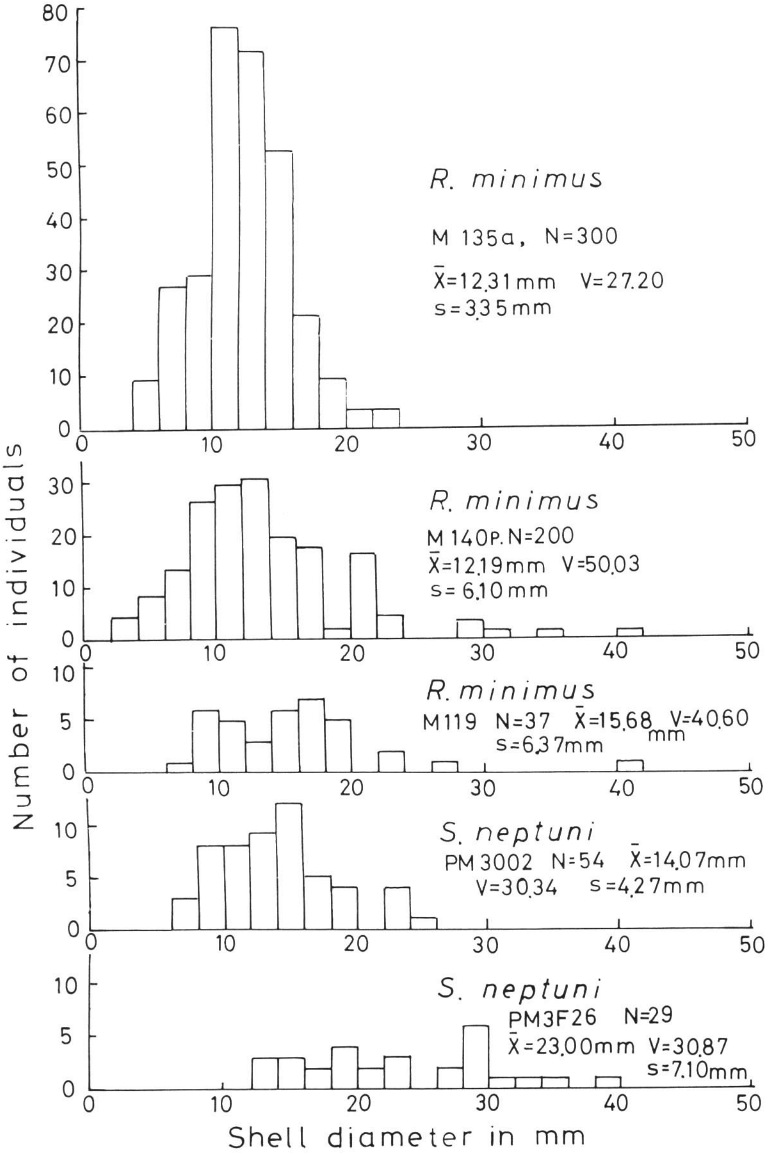


Fig. 4. Histograms of shell diameter in the selected 3 samples of *Reesidites minimus* and in the 2 samples of *Subprionocyclus neptuni* from the Upper Turonian of the Manji area. N: number of individuals in a sample, $\overline{X}$: mean shell diameter, V: coefficient of variation, s: standard deviation.

well as the species distribution pattern may give much reliable information to determine whether the objective ammonoid assemblage is virtually autochthonous or not. For that reason, the mode of occurrence of *R. minimus* and *S. neptuni* is described in detail in this chapter.

The preservation rates of spiral length of body chamber of both species in the selected 5 samples in contrast with those of smooth or weakly ornate ammonoids in other several samples are represented in Fig. 3.

The body chamber of both species is commonly well-preserved in every sample as compared with those of smooth or weakly ornate type species. In the case of *R. minimus,* the spiral length is gradually shortened with growth from about 250 to 200 degrees in accordance with the increase of rate of involution. The variation of spiral length of body chamber in the samples of *S. neptuni* is slightly larger than that in *R. minimus.* The length of body chamber of *S. neptuni* with a phragmocone diameter of about 10 mm ranges from 160 to 240 degrees in the sample PM 3002. In all probability, the body chamber of some individuals in this sample may has been secondarily damaged either during the process of fossilization or during the post-mortem transportation.

The frequency distributions of shell diameter of both species in the selected 5 samples with a large sample size are shown in Fig. 4. Except for the sample M 135a of *R. minimus,* the rest 4 samples of both species are composed of variously sized individuals (*see* Plate 1), and the coefficient of variation in each sample is relatively large. The size-distribution pattern of *R. minimus* in M 135a is characterized by the bell-shaped normal distribution curve without juvenile and large form of more than 25 mm in shell diameter.

As the adult form of *R. minimus* attains to the shell diameter of about 100 mm (MATSUMOTO, 1965b, p. 63), the three samples of *R. minimus* in M 135a, N 140p and M 119 are composed of immature shells only. However, several large individuals of the species, which are probably adult shells, were collected from the same stratigraphic level as the examined samples. In addition, most of smooth or weakly ornate type ammonoids in the examined samples are represented by small individuals (*see* Fig. 3).

We have identified 5 pieces of small aptychus in the samples, M 135a, b and M 140p from the Sannosawa together with many specimens of *R. minimus.* Furthermore, one individual of *R. minimus* with an aptychus in a body chamber was found out in the sample M 140p. Judging from the morphological identity among 5 separated aptychi and one autochthonous aptychus, the former 5 pieces may have been removed from the body chamber of *R. minimus.*

Comparison of Upper Turonian Ammonoid Assemblages of the Manji Area with those of other Areas

To compare the Upper Turonian ammonoid assemblages of the Manji area with those of other areas, the following 8 ammonoid samples from the Saku, Obira and

Oyubari areas are described in this chapter.

Samples S 1002 and S 1006: loc. T 680 in the lower course of the Abeshinai River, Saku area (lat. 44°44′ N, long. 142°2′ E; *see* MATSUMOTO, 1942, pl. 12). Coll. K. TANABE.

Sample S 2000: loc. T 46 in the middle stream of the southern tributary of the Saku-gakkonosawa, Saku area (lat. 44°44′ N, long. 142°1′ E; *see* MATSUMOTO, 1942, pl. 12). Coll. K. TANABE.

Sample R 2128: exposure in the upper course of the Obirashibe River, Obira area (lat. 44°6′ N, long. 142° E; *see* TANABE *et al.*, 1977, fig. 6). Coll. T. MATSUMOTO.

Sample R 2470d: exposure in the southern tributary of the Okufutamata Valley, Obira area (lat. 44°8′ N, long. 142°1′ E; *see* TANABE *et al.*, 1977, fig. 4). Coll. H. OKADA and K. TANABE.

Sample R 4034p: a float sample collected from the lower course of the Hifumizawa Creek, Obira area (lat. 44°4′ N, long. 141°59′ E; *see* TANABE *et al.*, 1977, fig. 9). Coll. H. HIRANO and K. TANABE.

Samples Y 1236a and Y 1229: exposures in the middle stream of the Isojiro-zawa Creek, tributary of the Yubari River, Oyubari area (lat. 43°5′ N, long. 142°7′ E). Coll. Y. HARAGUCHI.

These samples are stored in the type collection of Kyushu University. Every sample, except for R 4034p of the float sample, was separated from a single calcareous nodule, embedded in silty mudstone to fine sandy siltstone beds of the Turonian. The Middle to Upper Turonian in the Saku, Obira and Oyubari areas is characterized by silty mudstone, sandy siltstone, and intercalated sandstone and conglomerate lithofacies; hence it has been defined as a local lithostratigraphic unit, termed the Saku Formation by MATSUMOTO (1942). The above-mentioned 8 samples were collected from the upper part of the Saku Formation belonging to the Zone of *Inoceramus teshioensis* of Upper Turonian in age.

According to MATSUMOTO and OKADA (1973), the litho- and biofacies of the Turonian Saku Formation represent the intermediate facies between the inshore to nearshore shallow water facies and the offshore flysch one.

The species composition in these 8 samples is listed in Table 4. As is obvious in this table, the frequency of occurrence of the tetragonitids, desmoceratines and puzosiines, all of which belong to the smooth or weakly ornate morphotypes, is fairly large in every sample, as against rare in occurrence of the collignoniceratids.

Every sample including *R. minimus*- and *S. neptuni*-bearing samples (R 4034p and Y 1229) has a SIMPSON's (1949) index of concentration of less than 0.6; therefore the Upper Turonian ammonoid assemblages in the Saku, Obira and Oyubari areas may have a relatively large species diversity as compared with those in the Manji area. The Middle Turonian ammonoid assemblages in the former three areas have also large species diversities (TANABE, *in press*). Among the 21 species listed in Table 4 such species as *Scaphites planus* (YABE), *S. yokoyamai* JIMBO, *Otoscaphites puerculus* (JIMBO) and *Kossmaticeras* aff. *theobaldianum* (STOLICZKA) have not yet been found

Table 4. Species composition and SIMPSON's (1949) index of concentration in the 8 ammonoid samples from the Upper Turonian of the Saku, Obira and Oyubari areas, Hokkaido.

Species	Saku			Obira			Oyubari		
	S2000	S1006	S1002	R2128	R2470d	R4034p	Y1236a	Y1229	Total
Neophylloceras subramosum Spath							2	4	6
Damesites ainuanus Matsumoto	1					5	4	3	13
Tragodesmoceroides subcostatus Matsumoto	6	14	2	13	4				39
Yokoyamaoceras kotoi (Jimbo)						4			4
Kossmaticeras aff. *theobaldianum* (Stoliczka)						2			2
Mesopuzosia pacifica Matsumoto								2	2
M. cf. *yubarensis* (Jimbo)							1	3	4
M. sp.	4		1		1		1	4	11
Subprionocyclus neptuni (Geinitz)								16	16
Reesidites minimus (Hayasaka & Fukada)						4			4
Tetragonites glabrus (Jimbo)	13	11	12	4	4	1	9	5	59
Gaudryceras denseplicatum (Jimbo)	3	4		5	2	1	5	5	25
Anagaudryceras sp.						1			1
Madagascarites ryu Matsumoto & Muramoto					1			3	4
Scalarites sp.	2		1	1	2	2	2	1	11
Scaphites planus (Yabe)	1						1		2
S. yokoyamai Jimbo								1	1
Otoscaphites puerculus (Jimbo)					1				1
O. perrini (Anderson)								1	1
Sciponoceras intermedium Matsumoto & Obata								3	3
S. sp.						1			1
Number of specimens in each sample	30	29	16	23	15	21	25	51	210
Simpson's (1949) index of concentration	.24	.37	.56	.37	.13	.11	.18	.13	—

from the Upper Turonian of the Manji area.

The frequency of occurrence of ammonoids at family or subfamily level in the Upper Turonian regional sample groups from the Manji, Saku, Obira and Oyubari areas is summarized in Fig. 5.

Though the ammonoid faunal composition among the Saku, Obira and Oyubari samples is similar to one another, a considerable difference is observed between the Manji samples and the other regional sample groups.

It is worthy of notice that sample SN 2001 from the Manji area exceptionally resembles the samples of the Saku Formation with respect to species composition and species diversity.

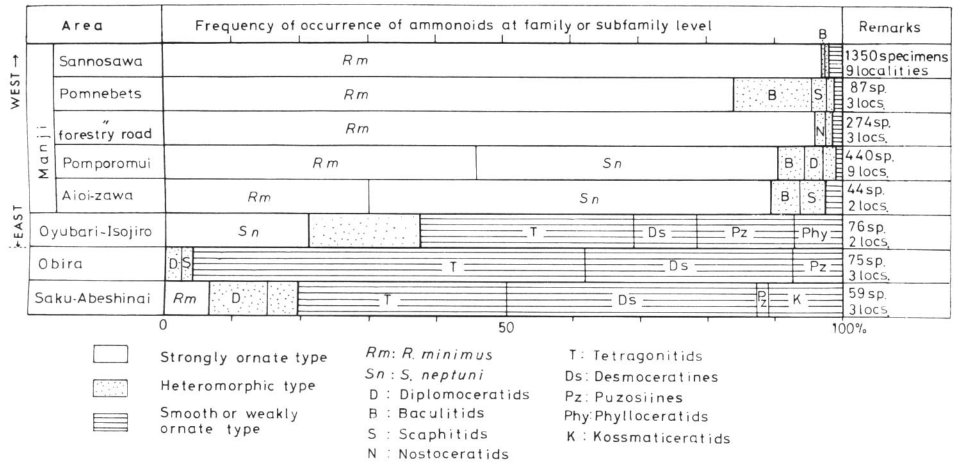


Fig. 5. Frequency of occurrence of ammonoids at family or subfamily level in several regional sample groups from the Upper Turonian of the Manji, Saku, Obira and Oyubari areas, Hokkaido.

Discussions

Relationship between morphotype occurrence and lithofacies.——Let us discuss the relationship between ammonoid morphotype occurrence and lithofacies on the grounds of TANABE's (*in press*) work on the Turonian ammonoid assemblages in the Saku, Obira and Oyubari areas in addition to the previously described results.

TANABE (*in press*) studied the distribution pattern and mode of occurrence of 29 ammonoid species in the Turonian of the Obira area based on about 3,000 individuals from 125 localities. The results are tabulated in Table 5.

As summarized in Tables 2, 4–5 and Fig. 3, several points of commonness on morphotype occurrence are observed between the Turonian of the Manji and Obira area.

The species belonging to the Tetragonitidae, Desmoceratidae and Phylloceratidae occur commonly throughout the Turonian sequence of the Obira area whereas they are rare in occurrence in the Upper Turonian of the Manji area. However, in both areas the frequency of occurrence of them at many localities is generally low, and the body chamber of them in almost every sample is secondarily damaged.

The heteromorphic ammonoids belonging to the Scaphitidae, Nostoceratidae and Diplomoceratidae are the most dominant group among the Turonian ammonoid fauna of the Obira area as well as of the Saku and Oyubari areas. Indeed, they occur abundantly in the silty mudstone to the fine sandy siltstone lithologies in a good state

Table 5. Mode of occurrence, preservation, relationship with lithofacies in occurrence, siphuncular strength, and suture complexity of ammonoid morphotypes in the Turonian of the Obira area, northwestern Hokkaido (adapted from TANABE, *in press*).

Ammonoid group	Species	Mode of occurrence	Preservation	Siphuncle & suture
Smooth or weakly ornate type	*N. subramosum*, *T. glabrus*, *G. denseplicatum* *D. ainuanus* etc.	Widespread & random distribution pattern regardless of litho-facies types. Frequency of occurrense at each locality is generally low.	Body chambers are frequently damaged.	Strong siphuncular strength & very complicated sutures.
Heteromorphic type	*O. puerculus*, *S. planus*, *S. yokoyamai*, *Eubostrychoceras* sp., *Hyphantoceras* sp. *Scalarites* sp. etc.	Relatively widespread & abundant occurrence in the silty mudstone to sandy siltstone facies.	Good state of preservation(scaphitids are found with complete apertural margin).*	Somewhat weak siphuncle & moderately complicated sutures.
Ornate type	*C. woollgari*, *S. bravaisianus*, *Y. yubarense*.	Limitative geographic distribution. Common occurrence in the fine sandstone to sandy siltstone facies	Good state of preservation.	weak siphuncle & simple sutures.

* footnote. More than 20 adult specimens of *O. puerculus* & *S. planus* with an aptychus in a body chamber have been identified from the Obira & Oyubari areas.

of preservation. It is interesting that such heteromorph species as *Sciponoceras intermedium, Madagascarites ryu, Otoscaphites perrini* and *Scaphites* aff. *subdelicatus*, all of common species in the Manji area, occur rarely in the Turonian of the Saku, Obira and Oyubari areas.

Most of the collignoniceratids are restrictedly distributed in the western part of the Obira area. In both Obira and Manji areas, the collignoniceratids are found abundantly in a good state of preservation. Except for *Scalarites* sp. and *M. ryu*, most of the heteromorphic species are rarely associated with the collignoniceratids in both Obira and Manji areas.

The above-mentioned characteristics in the mode of occurrence of the species in the Turonian of the Saku, Obira, Oyubari and Manji areas are well-represented by the similarity in the pattern of overlap in occurrence with other species between each two of the three morphotype groups, namely the smooth or weakly ornate type, the heteromorphic one and the strongly ornate one.

Typical examples of the pattern of overlap with other species in several morphotype species in the Obira and Manji areas are shown in Figs. 6–7 respectively.

In both areas the smooth or weakly ornate morphotype species such as the tetragonitids (*Tetragonites glabrus* (JIMBO) and *Gaudryceras denseplicatum* (JIMBO)) and desmoceratids (*Damesites ainuanus* MATSUMOTO, *Tragodesmoceroides subcostatus* MATSUMOTO and *Mesopuzosia* sp.) are characterized by the co-occurrence with other species, and their degree of interspecific overlap is generally high among the species of the same group. Except for *M. ryu* and *O. perrini*, most of the heteromorphic ammonoid species have also a high degree of overlap in occurrence with other species

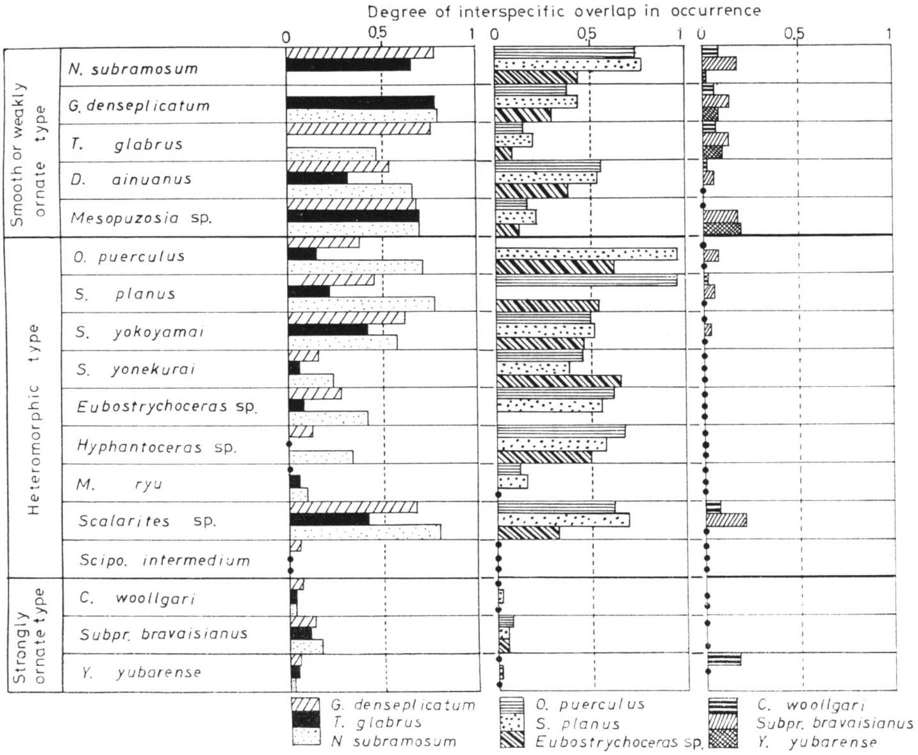


Fig. 6. Kimoto's (1967) index for the degree of overlap in occurrence with other species in the selected 9 species belonging to the three major morphotype groups, strongly ornate, heteromorphic, and smooth or weakly ornate types in the 22 ammonoid samples from the Middle Turonian of the Obira area, northwestern Hokkaido (adapted from Tanabe, *in press*).

of the same group. *O. perrini* and *M. ryu* have nearly the same pattern for interspecific overlapping, similar to those of the collignoniceratids in both Obira and Manji areas (*see* Fig. 8).

Main realm of post-mortem transportation and presumable habitats of the Turonian ammonoids in Hokkaido.——As already mentioned, various kinds of ammonoids occur abundantly or commonly throughout the Turonian sequences of various areas in the western meridional zone of Hokkaido. This fact may indicate that the distribution patterns of fossil ammonoids in Hokkaido reflect their main realms of post-mortem transportation. Here we discuss the problems of main realms of post-mortem transportation and presumable habitats of the Turonian ammonoids in Hokkaido in detail.

The main realms of distribution between the groups of such heteromorph species as *O. puerculus, S. planus, S. yokoyamai* and *Hyphantoceras* sp., and of the collignoniceratids do not coincide with each other. The former group is rich in occurrence

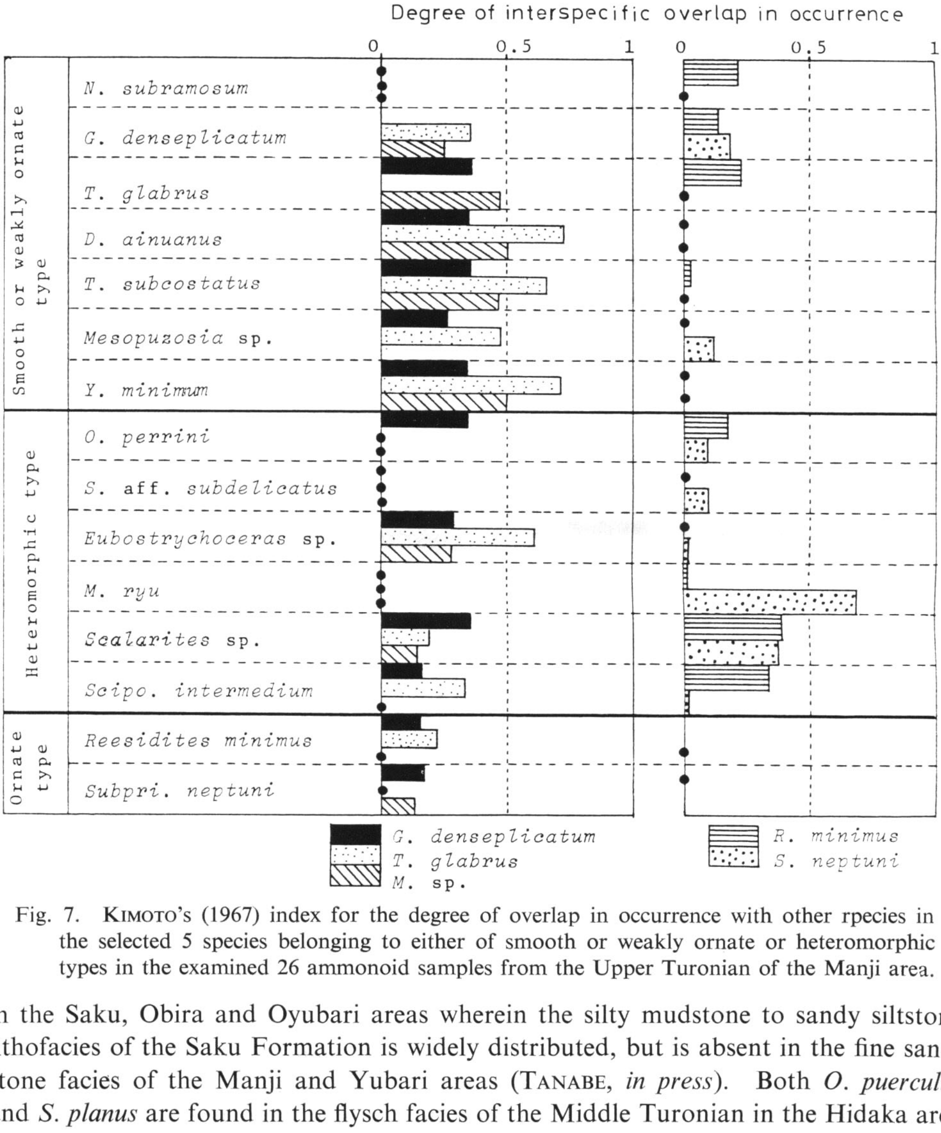


Fig. 7. KIMOTO's (1967) index for the degree of overlap in occurrence with other rpecies in the selected 5 species belonging to either of smooth or weakly ornate or heteromorphic types in the examined 26 ammonoid samples from the Upper Turonian of the Manji area.

in the Saku, Obira and Oyubari areas wherein the silty mudstone to sandy siltstone lithofacies of the Saku Formation is widely distributed, but is absent in the fine sandstone facies of the Manji and Yubari areas (TANABE, *in press*). Both *O. puerculus* and *S. planus* are found in the flysch facies of the Middle Turonian in the Hidaka area (OBATA *et al.*, 1973; TANABE, 1977), but their frequency of occurrence is low as compared with those in the Saku, Obira and Oyubari areas.

On the other hand, the collignoniceratids and such heteromorphs as *M. ryu*, *S. intermedium*, *O. perrini* and *S.* aff. *subdelicatus* are restrictedly distributed in the fine-grained sandstone to fine sandy siltstone facies in the western part of the marine Cretaceous basin of Hokkaido, especially in the Middle to the Upper Turonian of the Yubari and Ikushumbets areas (MATSUMOTO, 1965b; MATSUMOTO and HARADA, 1964) and in the Upper Turonian of the Manji area.

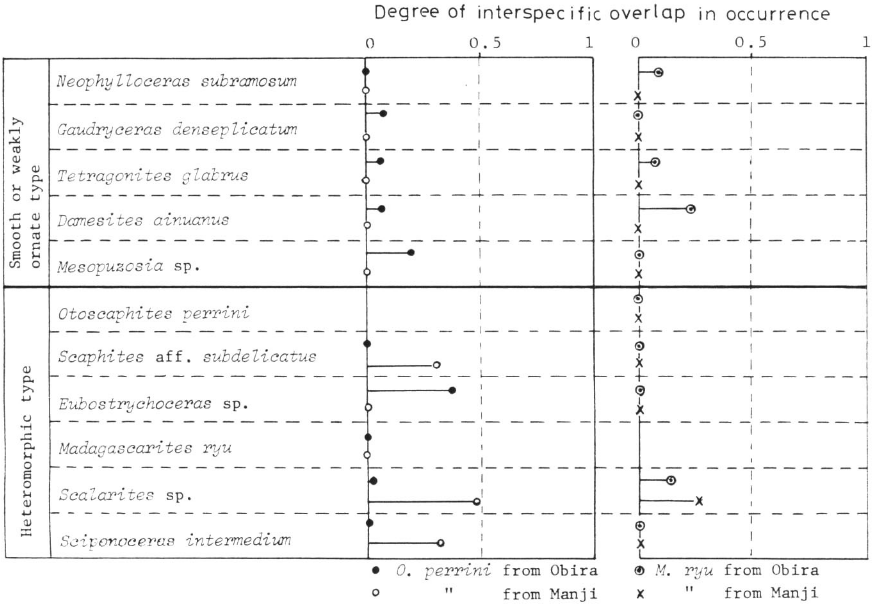


Fig. 8. KIMOTO's (1967) index for the degree of overlap in occurrence with other species in *Otoscaphites perrini* and *Madagascarites ryu*, both of heteromorphic type, in the 22 Middle Turonian ammonoid samples of the Obira area and in the 26 Upper Turonian ones of the Manji area. Data of the Obira samples are adapted from TANABE (*in press*).

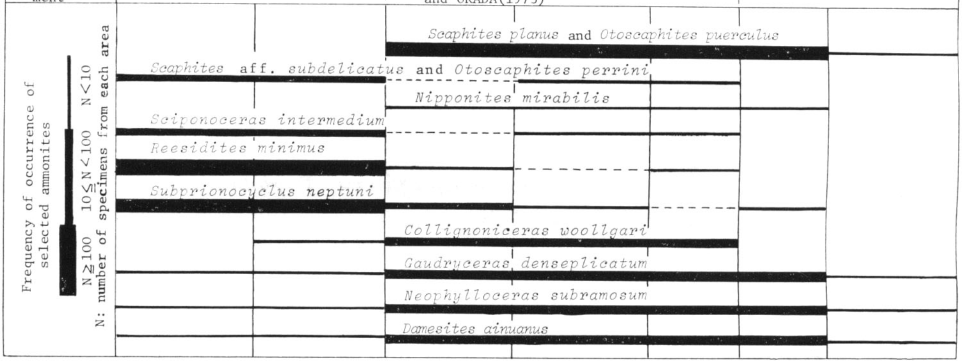
Such species as *Neophylloceras subramosum* SPATH, *T. glabrus*, *G. denseplicatum*, *D. ainuanus* and *T. subcostatus*, all of the smooth or weakly ornate morphotypes, have a wide geographic distribution from west (Manji, Yubari and Ikushumbets areas) to east (Hidaka area) in the marine Cretaceous basin of Hokkaido with a low frequency of occurrence at many localities regardless of lithofacies types.

On the ground of the results of this work and the previously published papers on the Turonian ammonoid assemblages in the Saku (MATSUMOTO, 1942; MATSUMOTO and OKADA, 1973), Obira (TANABE *et al.*, 1977; TANABE, *in press*), Oyubari (MATSUMOTO, 1942; HIRANO *et al.*, 1977; TANABE, *in press*), Yubari (MATSUMOTO and HARADA, 1964), Pombets-Ikushumbets (MATSUMOTO, 1965b), and Hidaka (OBATA *et al.*, 1973) areas, the frequency of occurrence of the selected 12 species belonging to several morphotypes in the Turonian of Hokkaido is summarized in Table 6. This table may well-represents the main realm of post-mortem transportation of each species.

Let us compare the above-mentioned data with the previously proposed models on ammonoid habitats. Although various opinions have been presented on the habitat and bathymetric distribution of ammonites, the three models, proposed by SCOTT (1940), MUTVEI (1975) and LEHMANN (1975) independently, are the note-worthy examples among them. The summary of these models and the expected distribution pattern of ammonoid thanatocoenoses from each model may be diagrammatically

Table 6. Summary of litho- and biofacies and frequency of occurrence of the selected 12 ammonoid species belonging to several morphotypes in the Turonian sequences of various areas of Hokkaido on the grounds of this work and previous papers. (1): OBATA and FUTAKAMI, 1975, 1977; MATSUMOTO and HARADA, 1964; this work, (2): MATSUMOTO, 1965b, (3): MATSUMOTO, 1942; MATSUMOTO and OKADA, 1973; this work, (4): MATSUMOTO, 1942; HIRANO *et al.*, 1977; TANABE, *in press*; this work, (5): TANABE *et al.*, 1977; TANABE, *in press*, (6): OBATA *et al.*, 1973.

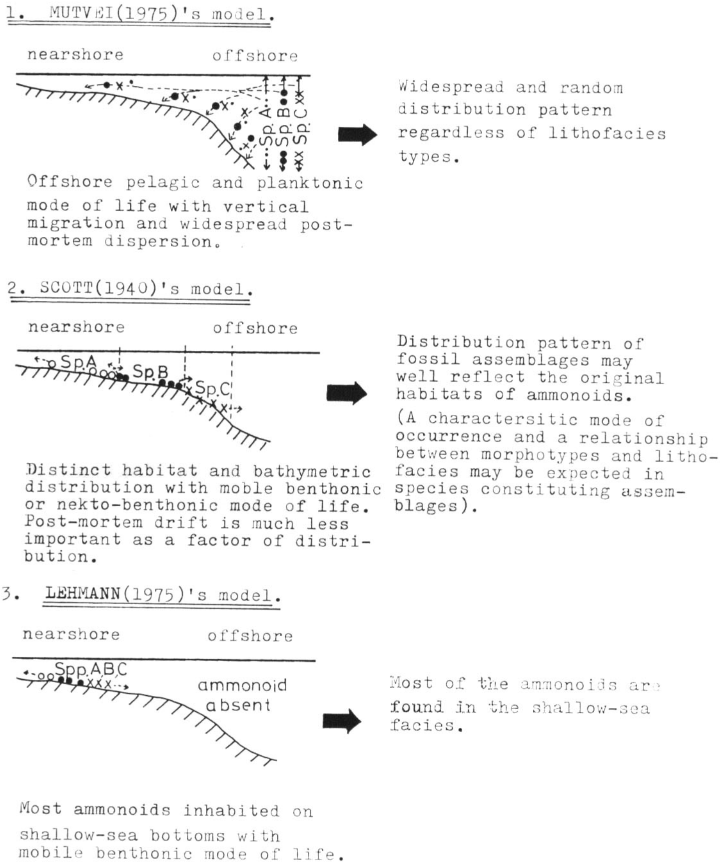
WESTERN PART ←			CENTRAL PART			→ EASTERN PART	
Area	Hatonosu-Manji (1)	Pombets (2)	Saku (3)	Oyubari (4)	Obira (5)		Hidaka-cho (6)
					S.W. area	N.E. area	
Thickness	140-360 m	340 m ±	470 m ±	600 m ±	ca. 700 m	1200 m	600-700 m
Lithology	mainly fine to medium sandstone with some lenses of conglomerate	fine sandstone & sandy siltstone with thin beds of conglomerate	siltstone, alternating sandstone & mudstone, & thin beds of sandst.	alternating fine sandstone & mudstone, silty mudstone & some beds of tuffite	fine sandstone, sandy siltstone with some lenses of conglomerate	silty mudstone & tuffite	mainly mudstone
Plant fragments	very abundant	abundant	common	common	abundant	common	rare
Ostreids	abundant	abundant	abundant	absent	rare	absent	absent
Trigonians	abundant	abundant	rare	absent	absent		absent
Presumable paleoenvironment	inshore to nearshore "shelf-like" facies		"intermediate" facies of MATSUMOTO and OKADA (1973)			offshore flysch facies	



represented in Fig. 9.

Among the three models, MUTVEI's one is well adapted in the smooth or weakly ornate morphotypes among the Turonian ammonoids in Hokkaido whereas LEHMANN's one explains the distribution and mode of occurrence of the collignoniceratids.

SCOTT's model (1940, fig. 8) is based on the relationship between morphotypes and lithofacies, and associated faunal character in the Albian of the Texas area. In this model the habitats of several morphotypes are distinctly separated from one another, and the post-mortem transportation or drift is much less important as a factor of distribution of thanatocoenoses because of the nektobenthonic or mobile benthonic mode of life of ammonoids. According to his model, species of *Phylloceras, Lytoceras, Tetragonites* and *Gaudryceras* live in a deeper water than the species of heteromorphic and sculptured types.



1. MUTVEI(1975)'s model.

Offshore pelagic and planktonic mode of life with vertical migration and widespread post-mortem dispersion.

Widespread and random distribution pattern regardless of lithofacies types.

2. SCOTT(1940)'s model.

Distinct habitat and bathymetric distribution with moble benthonic or nekto-benthonic mode of life. Post-mortem drift is much less important as a factor of distribution.

Distribution pattern of fossil assemblages may well reflect the original habitats of ammonoids. (A charactersitic mode of occurrence and a relationship between morphotypes and lithofacies may be expected in species constituting assemblages).

3. LEHMANN(1975)'s model.

Most ammonoids inhabited on shallow-sea bottoms with mobile benthonic mode of life.

Most of the ammonoids are found in the shallow-sea facies.

Fig. 9. Three different interpretations on habitats and bathymetric distribution of ammonoids proposed by Scott (1940), Mutvei (1975) and Lehmann (1975) respectively. The expected distribution pattern of post-mortem ammonoids from each model is also appended to this figure.

Scott's interpretation on bathymetric distribution of morphotypes has gained acceptance with such paleontologists as Ziegler (1967), Kauffman (1967), Wiedmann (1973), Matsumoto (1965a, 1977), Kanie (1977), Obata and Futakami (1977), and Tanabe (*in press*). Furthermore, works by Westermann (1971) and Tanabe (*in press*) on relative siphuncular strength in several morphotype species in contrast with the data on the relationship between depth ranges and pressure limits of siphuncular implosion among living *Nautilus, Sepia* and *Spirula* of Denton and Gilpin-Brown (1966, 1973), Raup and Takahashi (1966), and Collins and Minton (1967), may support the above-mentioned interpretation.

According to Scott's (1940) model, a characteristic mode of occurrence and distribution, which is intimately correlated with a definite marine environment, may be expected in the most species comprising the actual assemblages. Indeed, the distribution pattern and mode of occurrence of the collignoniceratids and most of the heteromorph species in the Turonian of Hokkaido are well-explained by SCOTT's model; however, the above-mentioned relation could not be observed in any species of smooth or weakly ornate morphotypes in the Turonian of Hokkaido (*see* Table 5).

TANABE (*in press*) gave the following two explanations for the distribution pattern of smooth or weakly ornate morphotypes in the Turonian of Hokkaido: 1. they were adapted to a wider area than the other species. Or, 2: Owing to the post-mortem transportation or drift extended to a wide area, their distribution pattern does not reflect their original habitats. In our present knowledge, the original habitat pattern and the wide post-mortem transportation or drift may both have controlled the distribution pattern of thanatocoenoses of smooth or weakly ornate morphotype species.

Although it is very difficult to accurately determine the absolute depth range and habitats of ammonoids, the above-described characteristics in the mode of occurrence and distribution pattern of ammonoids in the Turonian of Hokkaido may give much reliable information to estimate their approximate habitats.

Judging from the distinct mode of occurrence, good state of preservation of body chamber and occasional accompaniment of aptychi, most of the collignoniceratids and heteromorphs in the present material are autochthonous in a broad sense. The litho- and biofacies characters of the Turonian containing them may indicate that the collignoniceratids and most of the heteromorphs lived under the inshore to nearshore shallow water environment and the nearshore to offshore environment of shallow- to moderate depth respectively in Hokkaido at least in the Turonian age.

In contrast, most of the tetragonitids, phylloceratids and desmoceratids may have occupied wide habitats ranging from the nearshore to the offshore.

Furthermore, it can be postulated that the habitats of *R. minimus* and *S. neptuni* were segregated to a particular environment as represented by the Manji area in the Upper Turonian times. OBATA and FUTAKAMI (1977) assumed that the former species adapted under the less shallower sea environment than the latter one.

Lastly, we wish to discuss the mode of life in ammonoids from the viewpoint of assemblage paleoecology. Such workers as TRUEMAN (1941), HEPTONSTALL (1970), MUTVEI and REYMENT (1973), REYMENT (1973), MUTVEI (1975), WARD (1976), and WARD and WESTERMANN (1977) regarded the mode of life in most ammonoids as planktonic or nektoplanktonic, relying on the approximate determination of shell buoyancy and their fundamental similarity to living *Nautilus*. The following questions, however, may arise on the determination of mode of life in ammonoids from the analysis of shell buoyancy.

It is well-known that the living cephalopods have the density nearly equal to or slightly larger than that of the sea water (DENTON and GILPIN-BROWN, 1973), though they have various kinds of mode of life from nektonic to benthonic (BOLETZKY, 1977). Furthermore, the density of the shelly part greatly varies from a species to another among the living chambered cephalopods (DENTON and GILPIN-BROWN, 1973). As a matter of fact, it is at present impossible to estimate the volume of liquid within the chambers of living ammonoids. Judging from these lines of evidence, it is dangerous to determine the mode of life in ammonoids only from the analysis of shell buoyancy. In all probability, most living ammonoids may have nearly the same density as that of the sea water regardless of their mode of life.

As TANABE (*in press*) has already mentioned, the distribution pattern of ammonoids when alive was probably controlled by their mode of life. The great difference in shell morphology, mode of occurrence and distribution pattern among the three major morphotypes of the Turonian ammonoids in Hokkaido suggests the diversity of habitats and mode of life among them. At present, we assume that the collignoniceratids and some species of heteromorphs such as *S. planus, O. puerculus, M. ryu,* and *Nipponites mirabilis* YABE may have had a nektobenthonic or mobile benthonic mode of life and that the smooth or weakly ornate morphotypes such as *G. denseplicatum, T. glabrus, N. subramosum* and *Damesites ainuanus* may have had a planktonic or nektoplanktonic mode of life.

As a conclusion of this work, the presumable habitats, bathymetric distributions and main realms of post-mortem transportation of ammonoid morphotypes in Hokkaido in the Turonian age are diagrammatically illustrated in Fig. 10.

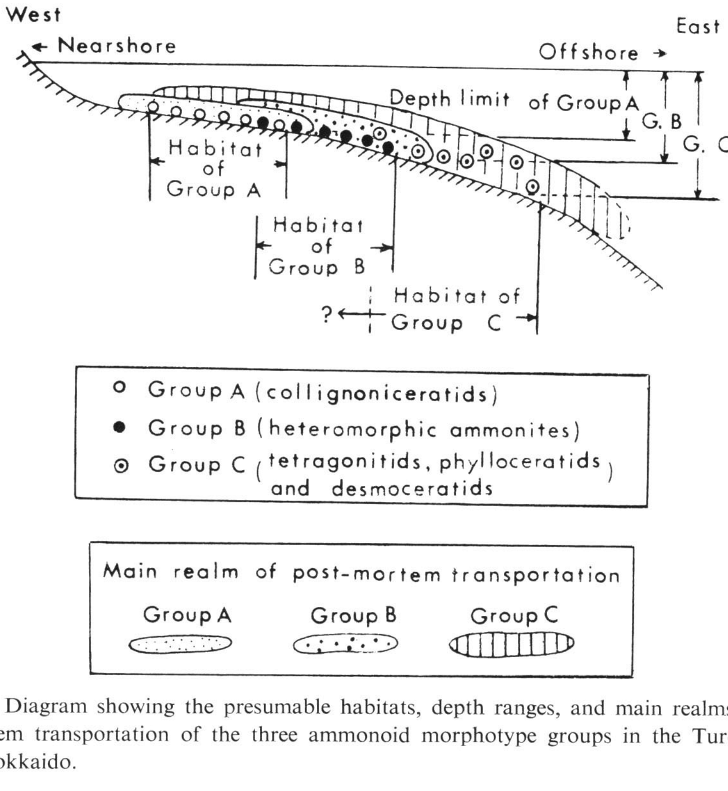


Fig. 10. Diagram showing the presumable habitats, depth ranges, and main realms of post-mortem transportation of the three ammonoid morphotype groups in the Turonian sea of Hokkaido.

Concluding Remarks

1. The Upper Turonian ammonoid assemblages of the Manji area, central Hokkaido are characterized by the dominant occurrence of the collignoniceratid species, *Reesidites minimus* and *Subprionocyclus neptuni*, and they have a relatively simple species diversity.
2. The faunal composition among the Upper Turonian ammonoid samples from the Saku, Obira and Oyubari areas is similar to one another; however, a considerable difference in species composition and species diversity is observed between the Manji samples and the other regional sample groups (*see* Fig. 5).
3. On the basis of the mode of occurrence and distribution pattern of a species, and the similarity in the pattern of interspecific overlap in occurrence among many species in the Turonian of various areas, the Turonian ammonoids of Hokkaido may be divided into the three major morphotype groups, namely the smooth or weakly ornate (the tetragonitids, desmoceratids, and phylloceratids), heteromorphic, and strongly ornate (the collignoniceratids) species groups.
4. Judging from the distinct mode of occurrence, restricted geographic distribution in the marine Cretaceous basin of Hokkaido, good state of preservation of body chamber and occasional accompaniment of aptychi, most of the collignoniceratids and heteromorphs in the present material are autochthonous in a broad sense. The litho- and biofacies characters of the Turonian containing them suggest that the former and latter groups may have had lived under the inshore to nearshore shallow water environment and the nearshore to offshore environment of shallow to moderate depth respectively (*see* Fig. 10).
5. The original habitat pattern and the wide post-mortem transportation or drift may both have controlled the distribution pattern of thanatocoenoses of smooth or weakly ornate type species. The species of this type may have occupied the wide habitats ranging from the nearshore to the offshore, because of their wide geographic distribution in the Cretaceous basin of Hokkaido with a low frequency of occurrence at many localities regardless of lithofacies types.
6. The great difference in shell morphology, mode of occurrence and distribution pattern among the three major morphotype groups of the Turonian ammonoids in Hokkaido may imply the diversity of habitats and mode of life among them.

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Explanation of Plate

Figs. 1–4. Mode of occurrence of *Reesidites minimus* (HAYASAKA and FUKADA) and *Subprionocyclus neptuni* (GEINITZ).

Fig. 1. Variously sized individuals of *Reesidites minimus* in the sample M 140 p (a float sample) from the creek of the Sannosawa. Coll.: K. TANABE & Y. MIYATA. ×1/2.

Fig. 2. Part of calcareous sandy nodule showing crowded mode of occurrence of *Ressidites minimus*. Sample: M 140 p. Coll.: K. TANABE & Y. MIYATA. ×1.

Fig. 3. Part of calcareous sandy nodule showing the occurrence of *Subprionocyclus neptuni*. Sample: PM 3F26, a float sample from the upper reach of the Pomporomui. Coll.: M. FUTAKAMI. ×1.

Fig. 4. Variously sized individuals of *Subprionocyclus neptuni* in the sample from loc. PM3002 along the upper reach of the Pomporomui. Coll.: M. FUTAKAMI. ×1.

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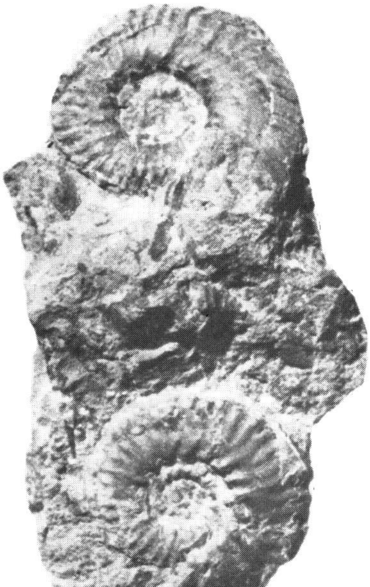

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