

Early Shell Growth in Some Upper Cretaceous Ammonites and Its Implications to Major Taxonomy*

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Introduction

Since BRANCO (1879–80) described the general characteristics of early shell growth in some ammonites, many works have been carried out on the ontogeny of siphuncle (SMITH, 1898; GRANDJEAN, 1910; TRUEMAN, 1920; SHIMIZU, 1929; SPATH, 1933; BÖHMERS, 1936) and the mode of early shell growth (ERBEN, 1966; MUTVEI, 1967; BIRKELUND, 1967; BIRKELUND & HANSEN, 1968; ERBEN *et al.*, 1969). More recently, the internal structural features of many ammonites have been studied from the viewpoint of major taxonomy by several Russian paleontologists (for example, DRUSHCHITS & KHIAMI, 1969, 1970; DRUSHCHITS & DOGUZHAYEVA, 1974; ZAKHAROV, 1974, 1977; DRUSHCHITS *et al.*, 1976, 1977a, b).

From these works, it has become clear that the study of ontogenetic development of internal shell structure is an important approach to the major classification and phylogeny of the Ammonoidea at or above superfamily level. However, further work is needed to determine exactly the taxonomic significance of internal structure, because the early ontogeny has been studied only on 200 to 220 species, which are little more than 2% of the approximately 10,000 ammonoid species (DRUSHCHITS & DOGUZHAYEVA, 1974).

In this paper we describe internal structural features and early shell growth in 28 species of the Upper Cretaceous Ammonoidea, and discuss their implications to major taxonomy.

* Contribution to the early ontogeny in modern and fossil chambered Cephalopoda, I

Material

The species studied in this paper are listed below, following ARKELL *et al.* (1957) as to their major taxonomic positions.

Suborder Phylloceratina

Superfamily Phyllocerataceae

Family Phylloceratidae

Neophylloceras subramosum SPATH—3 specimens (GK. H 8011, 8012, 5214)

Phyllopachyceras ezoense YOKOYAMA—2 specimens (GK. H 2055, 8042)

Suborder Ammonitina

Superfamily Acanthocerataceae

Family Acanthoceratidae

Yubariceras yubarensis MATSUMOTO, SAITO & FUKADA —1 specimen (GK. H 8037)

Family Collignoniceratidae

Collignoniceras woollgari (MANTELL)—1 specimen (GK. H 8013)

Subprionocyclus neptuni (GEINITZ)—2 specimens (NSM. PM 7415, 7432)

Reesidites minimus (HAYASAKA & FUKADA)—1 specimen (NSM. PM 9379)

Superfamily Desmocerataceae

Family Desmoceratidae

Tragodesmoceroides subcostatus MATSUMOTO—1 specimen (GK. H 8018)

Damesites ainuanus MATSUMOTO—1 specimen (GK. H 8019)

D. damesi (JIMBO)—5 specimens (GK. H 8020–8023, 4193)

D. semicostatus MATSUMOTO—2 specimens (GK. H 8017, 8039)

Hauericeras gardeni (BAILY)—1 specimen (GK. H 8025)

Mesopuzosia pacifica MATSUMOTO—1 specimen (GK. H 8016)

M. yubarensis (JIMBO)—2 specimens (GK. H 8038, 8040)

Kitchinites ishikawai (JIMBO)—3 specimens (GK. H 8041, 8015, 5197)

K. aff. japonicus SPATH—1 specimen (GK. H 8036)

Family Kossmaticeratidae

Yokoyamaoceras jimboi YABE—1 specimen (GK. H 8014)

Family Pachydiscidae

Eupachydiscus haradai (JIMBO)—1 specimen (GK. H 8024)

Pachydiscid, young, gen. et sp. indet.—1 specimen (NSM. PM 6172)

Superfamily Hoplitaceae

Family Placenticeratidae

Metaplacenticeras subtilistriatum (JIMBO)—1 specimen (NSM. PM 5840)

Suborder Lytoceratina

Superfamily Lytocerataceae

Family Tetragonitidae

Tetragonites glabrus (JIMBO)—2 specimens (GK. H 8029, 8030)

Gaudryceras denseplicatum (JIMBO)—3 specimens (GK. H 2158, 8026, 8028)

G. tenuiliratum YABE—3 specimens (GK. H 4195, 4196, 5019)

G. tenuiliratum YABE (var. *ornata* YABE)—1 specimen (GK. H 8027)

Anagaudryceras yokoyamai (YABE)—1 specimen (GK. H 8035)

Superfamily Scaphitaceae

Family Scaphitidae

Scaphites planus (YABE)—1 specimen (GK. H 5790)

S. pseudoequalis YABE—1 specimen (GK. H 8031)

Otoscapites puerculus (JIMBO)—1 specimen (GK. H 8033)

O. klamathensis (ANDERSON)—1 specimen (GK. H 8032)

Superfamily Turrilitaceae

Family Diplomoceratidae

Polyptychoceras sp.—1 specimen (GK. H 8034)

All specimens utilized were collected from selected areas of Hokkaido and South Sakhalin (Fig. 1), and are now stored in the Type Collections of Kyushu University (for GK. H specimens) and National Science Museum (for NSM. PM specimens). They were found in calcareous nodules in an excellent state of preservation. Among them, the following 7 specimens have already studied and illustrated by several authors with locality records: GK. H 4193, 2055, 5214 (MATSUMOTO & OBATA, 1955, pl. 30, figs. 2, 3, 5 respectively); GK. H 4195, 5197, 4196 (OBATA, 1960, pl. 15, figs. 1, 3, 5 respectively); GK. H 5019 (HIRANO, 1975, p. 24, fig. 6). Specimen, GK. H 8042 was collected from the same locality as GK. H 2055.

The locality and horizon of the remaining specimens are as follows.

GK. H 2158-3: loc. N 22z, an outcrop in the Miho River, Naibuchi area; hor., Upper Santonian; T. MATSUMOTO coll.

GK. H 8042: loc. N 182f, an outcrop in the Naibuchi Valley, Naibuchi area; hor., Lower Santonian; T. MATSUMOTO coll.

GK. H 8024: a specimen from a floated nodule in the middle stream of the Abeshinai River, Saku area; hor., Lower Campanian; K. TANABE coll.

NSM. PM 6172: a specimen from a floated nodule at loc. 1301F in the Saru River, Hidaka area; hor., Lower Campanian; H. TSUDA coll.

NSM. PM 5840: a specimen from a floated nodule in the Rubenosawa, the tributary of the Abeshinai River, Saku area; hor., Lower Campanian; T. MURAMOTO coll.

GK. H 8036: a specimen from a floated nodule in the upper stream of the Sakasagawa River, Haboro area; hor., Santonian; I. NAKAJIMA coll.

GK. H 8011-12, 8018: loc. R 2110d, an outcrop in the upper stream of the Obirashibe River, Obira area; hor., Middle Turonian; T. MATSUMOTO *et al.* coll.

GK. H 8013, 8033: loc. R 5505, an outcrop in the lower stream of the Nambuzawa, the tributary of the Obirashibe River, Obira area; hor. & coll. ditto.

GK. H 8014, 8017, 8039: loc. R 2673, an outcrop in the middle stream of the Jugosenzawa, the tributary of the Obirashibe River, Obira area; hor., Lower San-

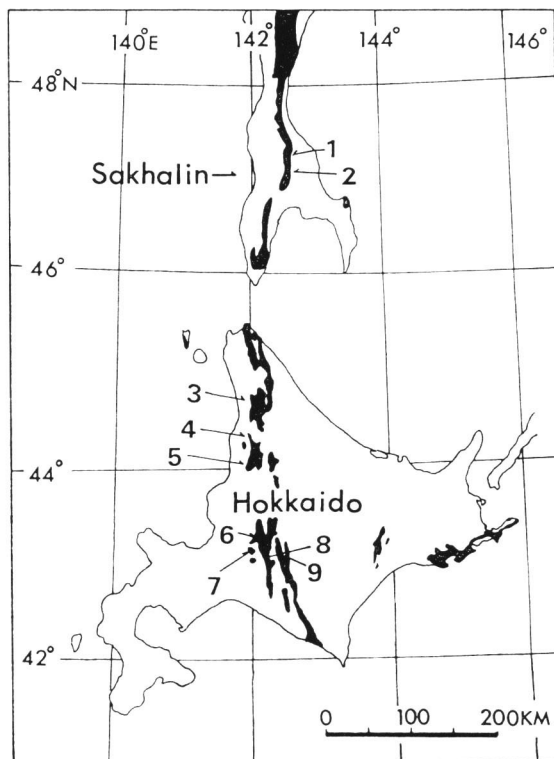


Fig. 1. Map of Hokkaido and south Sakhalin showing the post-Aptian Cretaceous outcrops and the sampling areas of ammonoid specimens examined. 1. Naibuchi, 2. Kawakami, 3. Saku, 4. Haboro, 5. Obira, 6. Ikushumbets, 7. Manji, 8. Oyubari, 9. Hidaka.

tonian; H. HIRANO & K. TANABE coll.

GK. H 8015, 8020–21, 8023, 8027, 8029, 8041: loc. R 2665, an outcrop in the middle stream of the Jugosenzawa, the tributary of the Obirashibe River, Obira area; hor. & coll. ditto.

GK. H 8022, 8034: specimens from a floated nodule in the middle stream of the Sakumazawa, the tributary of the Obirashibe River, Obira area; hor. & coll. ditto.

GK. H 8016: a specimen from a floated nodule in the middle stream of the Nakanembets River, Obira area; hor., Middle Turonian; T. MATSUMOTO *et al.* coll.

GK. H 8028: loc. R 6072a, a river-side cliff near Takimibashi, middle stream of the Obirashibe River, Obira area; hor. & coll. ditto.

GK. H 8030: loc. R 2113h, an outcrop in the upper stream of the Obirashibe River, Obira area; hor. & coll. ditto.

GK. H 8038: a specimen from a floated nodule in the Sekitannaizawa, the tributary of the Shimokinembets River, Obira area; hor., Turonian; K. TANABE coll.

GK. H 8019, 8037, 8040: specimens from a floated nodule in the Sannosawa, the tri-

butary of the Shimokinembets River, Obira area; hor., Middle Turonian; Y. MIYATA coll.

GK. H 8031: a specimen from a floated nodule in the Gonosawa, the tributary of the Pombets River, Ikushumbets area; hor., Lower Coniacian; T. MATSUMOTO coll.

GK. H 8032: loc. IK 2141r, an outcrop in the Gonosawa, the tributary of the Pombets River, Ikushumbets area; hor. & coll. ditto.

GK. H 8025: a specimen from a floated nodule in the Ikushumbets Valley (about 800 m east from the Katsurazawa Dam), Ikushumbets area; hor., Santonian; T. MATSUMOTO coll.

NSM. PM 9379: loc. RN 8001, an outcrop along the Pomnebets forestry road, Manji area; hor., Upper Turonian; I. OBATA & M. FUTAKAMI coll.

NSM. PM 7415, 7432: loc. PM 3002, an outcrop in the upper stream of the Pomporomui River, Manji area; hor. & coll. ditto.

GK. H 5790: loc. Y 5201a, an outcrop in the lower stream of the Hakkinzawa, the tributary of the Yubari River, Oyubari area; hor., Middle Turonian; T. MATSUMOTO coll.

Method of Study

To study the internal structural characteristics of a species, most specimens were cut or polished along the median plane. Only specimen, GK. H 8035 of *Anagaudryceras yokoyamai* was examined in a cross section. The following 11 internal structural elements have been examined on the median sectional specimens: (1) protoconch, (2) prosiphon, (3) partial septa, (4) caecum, (5) proseptra, (6) flange, (7) nepionic constriction, (8) ammonitella, (9) siphuncle, (10) septa, and (11) septal necks. The observation was performed using a WILD microscope and a profile projector (Nikon Co.) with magnifications, X40–X200. For three specimens of *Kitchinites* aff. *japonicus*, *Yubariceras yubarensis* and *Polyptychoceras* sp., the examination was restricted to the morphology of septal necks, because of unfavourable preservation of early growth stage.

The measurements were carried out on the protoconch size, ammonitella size, prosiphonal length, siphuncular diameter, and radius vector of a spiral with a micrometer of 1 μm accuracy, attached to a profile projector. The latter two characters were measured at intervals of 0.25π . To describe the microstructure of several elements, a result of the study through scanning electron microscope on the three specimens of *Damesites semicostatus*, *Mesopuzosia yubarensis* and *Eupachydiscus haradai* (GK. H 8024, 8038–39) by TANABE *et al.* (*in press*) is partly cited into this paper. Furthermore, three drawings in Fig. 4 are adapted from SHIMIZU (1929). The terminology of the internal structure used in the text is based on BRANCO (1879–80), GRANDJEAN (1910), SHIMIZU (1929), and DRUSHCHITS & KHIAMI (1969). The basic morphology and measurements of ammonoid internal shell structure are diagrammatically illustrated in Fig. 2.

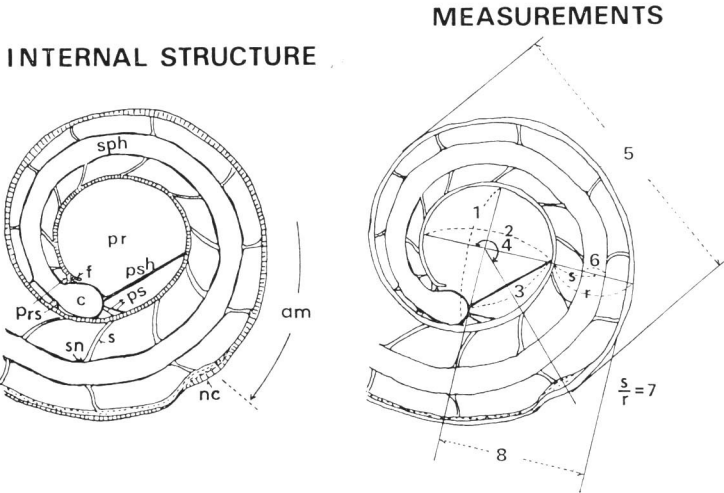


Fig. 2. Basic morphology and measurements of ammonoid internal shell structure in the median section. Terminologies are cited from BRANCO (1879–80), GRANDJEAN (1910), SHIMIZU (1929), and DRUSHCHITS & KHIAMI (1969). pr: protoconch, psh: prosiphon, c: caecum, ps: partial septa, prs: proseptum, f: flange, sph: siphuncle, am: ammonitella, nc: nepionic constriction, s: septum, sn: septal neck. 1, 2. maximum and minimum diameters of protoconch, 3. length of prosiphon, 4. spiral length of ammonitella, 5. ammonitella size, 6. siphuncular diameter, 7. parameter showing position of siphuncle, 8. radius vector of a spiral.

Descriptions

Before starting the descriptions, the measurements of several characters in the specimens examined are listed in Table 1.

Protoconch: The internal shell structure in the ammonitella stage of selected species is shown in Fig. 3 and Plate 1. Every species examined has a nearly spherical to slightly elliptical empty protoconch in the median section; the ratio of minimum diameter to maximum one is more than 0.79 (see Table 1). The protoconch is of intermediate size in the phylloceratids, and rather small in the Ammonitina and the scaphitids. In contrast, shells of the tetragonitids have a much larger protoconch of more than 0.66 mm in maximum diameter. According to HIRANO (1975, 1978), the intra-specific variation of protoconch size in *Gaudryceras* is smaller than those of other characters. Therefore, it is probably certain that species of the Tetragonitidae have an extremely larger protoconch as compared with other groups.

Prosiphon: The prosiphon is well preserved in the specimens belonging to the following 15 species: *Neophylloceras subramosum* (GK. H 8012), *Phyllopachyceras ezoense* (H 8042), *Damesites ainuanus* (H 8019), *D. damesi* (H 8020, 8022–23), *D. semicostatus* (H 8039, 8017), *Mesopuzosia pacifica* (H 8016), *Kitchinites ishikawai* (H 8015),

Hauericeras gardeni (H 8025), *Eupachydiscus haradai* (H 8024), pachydiscid gen. et sp. indet. (NSM. PM 6172), *Gaudryceras tenuiliratum* (H 4196), *G. denseplicatum* (H 2158), *Scaphites planus* (H 5790), *S. pseudoequalis* (H 8031), and *Otoscapites klamathensis* (H 8032) (Figs. 3, 4; Pl. 1). In these species it is characterized by a fine horny structure, extending from protoconch wall to adapical part of caecum. In *G. tenuiliratum* and *E. haradai* its diameter tends to be enlarged toward caecum (Fig. 4-3, 7; Pl. 1, Figs. 2, 5). SHIMIZU (1929, pl. 1, figs. 2-5; pl. 2, figs. 1-2, 5) also described the same phenomenon in several tetragonitids, *Neophylloceras ramosum* (MEEK) and *Reesidites minimus*. Furthermore, the prosiphon in GK. H 8023 of *D. damesi* spreads into two branches near the caecum (Pl. 1, Fig. 6).

Comparing the results of observation on the prosiphon on species of the three major taxonomic groups, it can be stated that the phylloceratids and the lycoceratids both have an extremely short and adorally convex prosiphon with the ratio of this length to protoconch diameter of less than 0.3, in contrast to a long and nearly straight prosiphon of the Ammonitina (the length to protoconch size is more than 0.3) (Fig. 4, Table 1, Pl. 1). According to the SEM photographs of the portion in *D. semicostatus* and *E. haradai* by TANABE *et al.* (*in press*, here cited in Pl. 2, Figs. 1-2, 4-5), it is represented by a fine horny tube of less than 5 μm in diameter, which is directly connected with the horny layer of caecum.

Partial septa: SHIMIZU (1929) recognized two or three fine prosiphon-like calcareous (?) tubes at ventral side of caecum in several Upper Cretaceous ammonites from South Sakhalin and Hokkaido (three examples are reproduced to Fig. 4), and termed the structure as partial septa. In the specimens examined, two partial septa are well preserved in *G. tenuiliratum* (GK. H 4196) and *N. subramosum* (GK. H 8012) (Fig. 4-1, 3; Pl. 1, Figs. 1-2). The partial septa of the two species somewhat resemble the prosepata in its position, but are easily distinguished for their restricted development at the ventral side of caecum. In the examined specimens of the Ammonitina, they are absent, although the prosiphon is well preserved in some of them. The similar structure has already been noticed in some Jurassic and Cretaceous ammonites (*Arietites kridion*, *Amaltheus margaritatus*, *Ludwigia opelina*; GRANDJEAN, 1910, figs. 7-9; *Phyllopachyceras* sp., *Tetragonites duvalianus*; DRUSHCHITS & DOGUZHAYEVA, 1974, figs. 1, 5). As SHIMIZU (1929) has already pointed out, partial septa are more closely similar to a prosiphon than prosepata for their form and position; accordingly, further work is required to examine the microstructural similarity or dissimilarity between the two.

Caecum: As shown in Fig. 3 and Pl. 1, the outline of the caecum in the longitudinal section is semi-circular in the Lycoceratina, but is elliptical or rounded in the Ammonitina and the Phylloceratina. The wall of caecum in every specimen examined is composed of an outer thin calcareous and an inner thick horny layers. According to the SEM observation of the portion by TANABE *et al.* (*in press*), the outer layer in *D. semicostatus*, *E. haradai*, and *M. yubarensis*, about 5 μm thick, has a massive microstructure, while the inner one, more than 20 μm thick, is composed of multi-layered

Table 1. Measurement data of selected internal shell characters in the specimens examined.
 *Cited from TANABE (1977a). **Cited from TANABE (1977b). N: number of specimens.

Species	Specimen	Protoconch		Prosiphon		Ammonitella			Ventral position of siph. (deg.)	
		Maximum diameter Pl (mm)	Minimum diameter Ps (mm)	Ps/Pl	Length (mm)	length Pl	Maximum size (mm)	Number of speta		Spiral length (degrees)
Phylloceratina										
<i>N. subramosum</i>	H 8011	0.535	0.433	0.81	?	?	0.902	10	270	660
"	H 8012	0.540	0.447	0.83	0.116	0.215	0.970	10	270	738
"	H 5214	0.662	0.572	0.86	?	?	1.152	?	270	630
<i>P. ezoense</i>	H 8042	0.559	0.489	0.88	0.130	0.266	1.303	12	377	515
"	H 2055	0.576	0.468	0.82	?	?	1.280	12	376	500
Ammonitina										
<i>C. woolligari</i>	H 8013	0.437	0.368	0.84	?	?	0.820	9	275	824
<i>R. minutus</i>	PM 9379	0.458	0.452	0.99	?	?	1.004	9	333	702
<i>S. neptuni</i>	PM 7415	0.419	0.369	0.88	?	?	0.760	8	270	765
"	PM 7432	0.445	0.397	0.89	?	?	0.735	7	280	?
<i>T. subcostatus</i>	H 8018	0.472	0.406	0.86	?	?	0.924	9	314	540
<i>D. ainuanus</i>	H 8019	0.378	0.327	0.87	0.152	0.402	0.730	9	290	655
<i>D. semicostatus</i>	H 8017	0.468	0.405	0.87	?	?	0.912	9	320	630
"	H 8039	0.388	0.346	0.89	0.255	0.657	0.764	9	315	640
<i>D. damesi</i>	H 8021	0.421	0.362	0.86	?	?	0.832	10	315	655
"	H 8022	0.460	0.392	0.85	0.146	0.318	0.907	9	335	640
"	H 8023	0.425	0.388	0.91	0.176	0.414	0.912	9	307	660
"	H 8020	0.451	0.429	0.95	0.258	0.572	0.854	11	324	658
"	H 4193	0.444	0.398	0.90	?	?	0.911	10	360	647
<i>M. pacifica</i>	H 8016	0.432	0.409	0.95	0.284	0.657	0.829	9	310	525
<i>K. ishikawai</i>	H 5197	0.607	0.515	0.85	?	?	0.939	9	297	450
"	H 8015	0.536	0.490	0.91	0.283	0.527	0.896	8	305	475
<i>H. gardeni</i>	H 8025	0.495	0.392	0.79	0.150	0.303	0.700	9	315	847
<i>Y. jimboi</i>	H 8014	0.534	0.492	0.92	?	?	0.972	10	340	360

<i>E. haradai</i>	H 8024	0.525	0.511	0.97	0.250	0.476	1.065	11	333	528
Pachydiscid	PM 6172	0.463	0.416	0.90	0.271	0.585	0.798	11	300	520
<i>M. subtilistriatus</i>	PM 5840	0.532	0.494	0.93	?	?	1.088	10	350	625
Lytoceratina										
<i>G. denseplicatum</i>	H 8026	0.862	0.752	0.87	?	?	1.653	11	335	?
"	H 8028	0.800	0.776	0.97	?	?	1.510	?	320	?
"	H 2158	0.706	0.646	0.92	0.110	0.156	1.387	11	328	70
<i>G. tenuiliratum</i>	H 5019	0.777	0.714	0.92	?	?	1.603	10	374	?
"	H 4195	0.760	0.742	0.98	?	?	1.553	10	350	50
"	H 4196	0.777	0.752	0.97	0.114	0.147	1.645	12	345	55
" (var. <i>ornata</i>)	H 8027	0.714	0.635	0.89	?	?	1.337	11	360	38
<i>T. glabrus</i>	H 8029	0.662	0.619	0.94	?	?	1.348	11	345	39
"	H 8030	0.911	0.852	0.94	?	?	1.880	11	335	?
<i>S. planus</i>	H 5790	0.550	0.470	0.89	0.083	0.151	0.888	8	280	15
"	N=468*	0.399					0.730			
		?					?			
		0.576					0.949			
<i>S. pseudoaequalis</i>	H 8031	0.448	0.413	0.92	0.120	0.268	0.790	8	295	40
"	N=20**	0.351					0.641			
		?					?			
		0.460					0.800			
<i>O. puerculus</i>	H 8033	0.540	0.509	0.94	?	?	0.900	9	285	20
"	N=469*	0.425					0.714			
		?					?			
		0.581					0.920			
<i>O. klamathensis</i>	H 8032	0.464	0.450	0.97	0.110	0.237	0.820	9	285	10
"	N=28**	0.366					0.670			
		?					?			
		0.475					0.825			

horny membranes.

Proseptum or proseptra: Every species examined has one or two proseptra around the base of caecum (Fig. 4). The proseptra are easily distinguished from the succeeding first septum in that they are connected with the outer calcareous layer of a caecum wall.

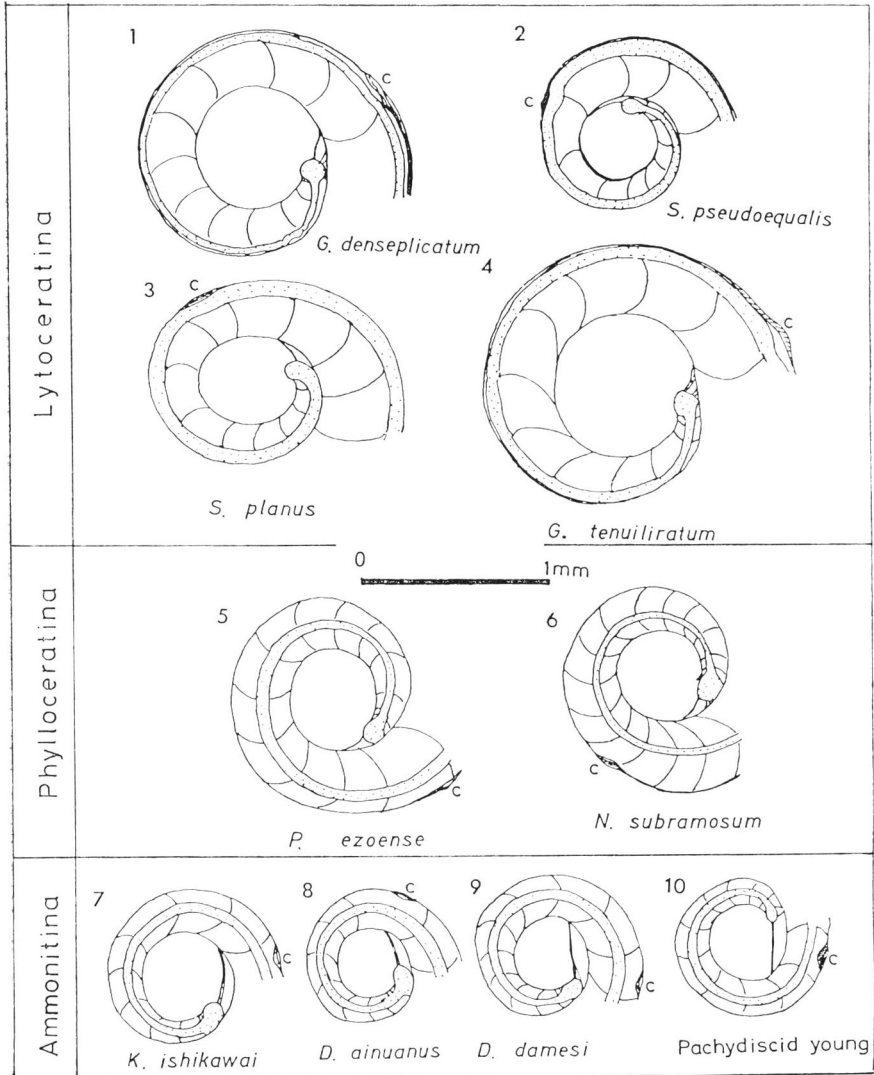


Fig. 3. Drawings showing the early stage of selected species in the median section. c: nepionic constriction. 1. GK. H 2158, 2. H 8031, 3. H 5790, 4. H 4196, 5. H 8042, 6. H 8012, 7. H 8015, 8. H 8019, 9. H 8023, 10. NSM. PM 6172.

Flange: The flange, that is the adapical extension of protoconch wall, is restrictedly preserved in specimen GK. H 8012 of *N. subramosum* (Fig. 4-1, Pl. 1, Fig. 1). It is about 20 μm in length, and gently curved toward the inside of protoconch. In other specimens examined, the protoconch wall is directly linked with the proseptra and the outer calcareous layer of caecum wall (Fig. 4).

Nepionic constriction: A conspicuous nepionic (=primary) constriction exists between the first and second whorls of every specimen studied (Fig. 3, Pls. 3-5). It is represented by an abrupt thickening of the inner nacreous layer of ventral shell wall, which begins to appear just before the constriction, as BIRKELUND (1967), BIRKELUND & HANSEN (1968), ERBEN *et al.* (1969), and DRUSHCHITS & DOGUZHAYEVA (1974) have already demonstrated in many ammonites. The constriction also marks an interrup-

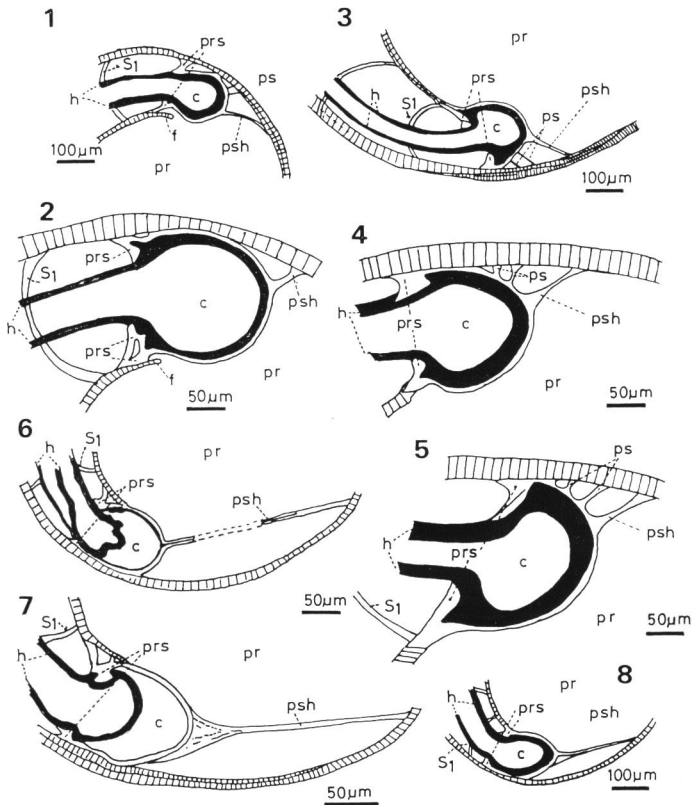


Fig. 4. Drawings showing the morphology of early internal shell structure in selected species in the median section. 1. *N. subramosum* (GK. H 8012), 2. *P. ezoense* (adapted from SHIMIZU, 1929, pl. 1, fig. 6), 3. *G. tenuiliratum* (H 4196), 4. *G. denseplicatum* (adapted from SHIMIZU, 1929, pl. 1, fig. 3), 5. *Anagaudryceras limatum* (adapted from SHIMIZU, 1929, pl. 1, fig. 4), 6. *D. semicostatus* (H 8039), 7. *E. haradai* (H 8024), 8. *D. damesi* (H 8023). S₁: first septum, h: horny membranes. For other abbreviations in this figure see the explanations of Fig. 2.

tion in growth of radius vector of a spiral in many species.

The ontogenetic appearance of the constriction varies among species examined. As summarized in Table 1, it occupies between 270° and 377° of the total rotation angle from the axis of coiling in the Phylloceratina, between 270° and 360° in the Ammonitina, and between 280° and 374° in the Lytoceratina. At family level, the angle ranges from 270° to 333° in the collignoniceratids, and from 290° to 360° in the desmoceratids. In contrast, the tetragonitids have much larger angles ranging from 320° to 374° . Although we have not examined sufficient material, the angle is nearly constant within the specimens of the same species (Table 1). The results almost coincide with SHIMIZU's (1929) data on 11 Upper Cretaceous ammonites, and both suggest that the position of nepionic constriction is stable in each species. GRANDJEAN (1910) interpreted that the nepionic constriction angle has progressively decreased in the evolutionary history of the Ammonoidea. Such evidence, however, could not be ascertained in the Upper Cretaceous ammonites studied.

Ammonitella: The term ammonitella was proposed by DRUSHCHITS & KHIAMI (1969) for a conch with a nepionic constriction at its aperture. As listed in Table 1, the maximum size of ammonitella in the median section ranges from 0.902 to 1.303 mm in the Phylloceratina, from 0.700 to 1.088 mm in the Ammonitina, and from 0.641 to 1.880 mm in the Lytoceratina. At family level, all of the collignoniceratids, desmoceratids, and scaphitids have a more or less small ammonitella of less than 1 mm in diameter, in contrast to the extremely large ammonitella of more than 1.3 mm in the tetragonitids. The ammonitellas of the phylloceratids, kossmaticeratid, and hoplitid are of intermediate size. The ratio of ammonitella size to protoconch diameter remains constant (ca. 1.6–1.7) among the specimens examined; in other words, a significant positive linear relationship exists between the dimensions of the two characters at interspecific level (Fig. 5). We have also confirmed the significant linear relationship within selected samples of the scaphitids, depending on the basic data of TANABE (1977a, figs. 9, 10; 1977b, fig. 5) (Fig. 6). These results may be important to consider the early ontogeny of ammonites. According to the hypothetical model of ERBEN *et al.* (1969, fig. 5), a protoconch and succeeding whorl(s) up to a nepionic constriction respectively correspond to air and living chambers of a living ammonite in the phase of metamorphosis from larval to post-larval stages. In this case, a constant volume ratio between air and living chambers is necessary to maintain the neutral buoyancy (= planktonic mode of life) of an animal. For this reason, Figs. 5–6 seem to support their model.

Septa: The ammonitella in the species examined has 7 to 12 adorally convexed and regularly-spaced septa (Table 1). In every specimen belonging to the three collignoniceratid species, *C. woollgari*, *S. neptuni*, and *R. minimus*, the approximation of two contiguous septa periodically occurs from the end of the ammonitella stage to the fourth or fifth whorls (Pl. 5, Fig. 1), though such a periodical pause of septal growth could not be ascertained in other ammonites studied.

Siphuncle: The siphuncle is initially located at a central or subcentral part of a

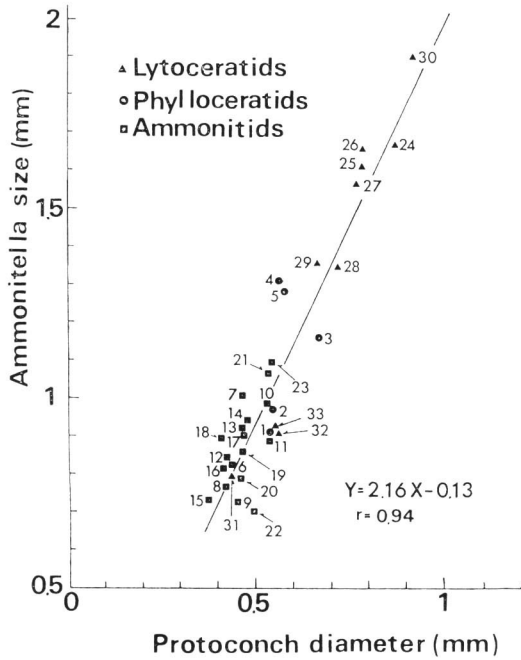


Fig. 5. Double scatter diagram showing the interspecific relationship between protoconch diameter and ammonitella size. Regression line with a least square method is indicated in this figure. r : correlation coefficient. 1–3. *N. subramosum* (GK. H 8011, 8012, 5214), 4–5. *P. ezoense* (H 8042, 2055), 6: *C. woollgari* (H 8013), 7. *R. minimus* (NSM. PM 9379), 8–9. *S. neptuni* (PM 7415, 7432), 10. *Y. jimboi* (H 8014), 11. *K. ishikawai* (H 8015), 12. *M. pacifica* (H 8016), 13: *D. semicostatus* (H 8017), 14. *T. subcostatus* (H 8018), 15. *D. ainuanus* (H 8019), 16–19. *D. damesi* (H 8021–8023, 8020), 20: pachydiscid gen. et sp. indet. (PM 6172), 21. *E. haradai* (H 8024), 22. *H. gardeni* (H 8025), 23. *M. subtilistriatum* (PM 5840), 24. *G. denseplicatum* (H 8026), 25–28. *G. tenuiliratum* (H 5019, 4196-1, 4196-2, 8027), 29–30. *T. glabrus* (H 8029–8030), 31. *S. pseudoequalis* (H 8031), 32. *S. planus* (H 5790), 33. *O. puerculus* (H 8033).

whorl in every species examined, but gradually or abruptly approximates its position to the ventral side as the shell grows. Fig. 7 summarizes the ontogenetic change of siphuncle position with respect to total rotation angle of a spiral in selected species. As shown in this figure and Pls. 3–5, in both the Phylloceratina and the Ammonitina the siphuncle reaches the marginal position at some stage between the end of the second whorl and the middle of the third one. At family level, the marginal approximation of siphuncle in the desmoceratids is attained before the middle stage of the second whorl, but it is prolonged up to the end of the third one in the collignoniceratids and the pachydiscids.

In the 9 lytoceratid species studied, the siphuncle occupies a subcentral position around the second-third septa (less than 45° in spiral length of a whorl), and then rapid-

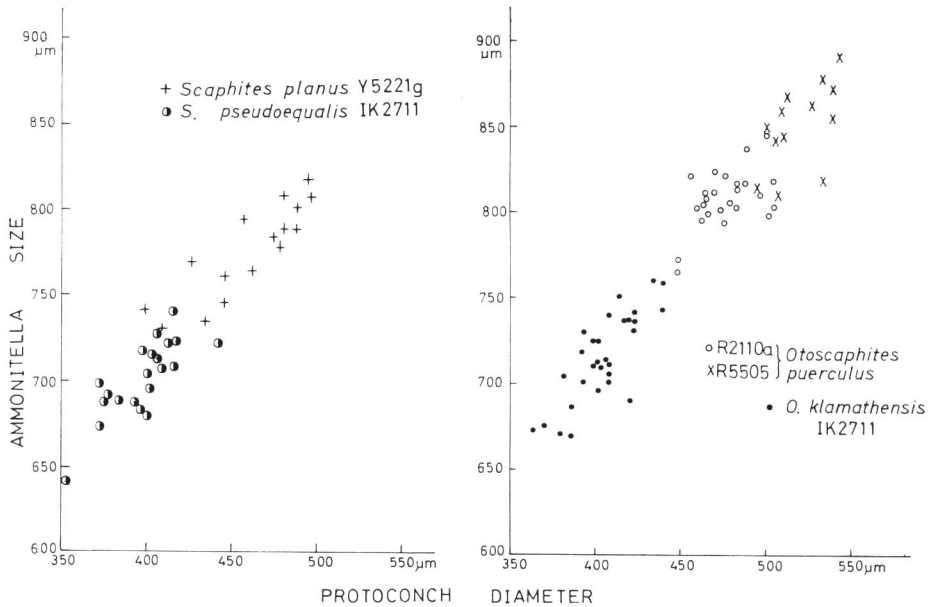


Fig. 6. Double scatter diagrams showing the intraspecific relationship between protoconch diameter and ammonitella size in selected samples of four scaphitids. The basic data of this figure are cited from TANABE (1977a, figs. 9, 10; 1977b, fig. 5).

ly shifts its position toward the ventral side with growth.

Although the growth of siphuncular diameter to radius vector of a spiral is negative allometric in every species examined, such species as *M. subtilistriatum*, *R. minimus*, *C. woollgari*, *O. puerculus*, and *S. planus*, all of which occur in the inshore to nearshore shallower water facies (TANABE *et al.*, 1978), have a broader siphuncle than the other offshore-type ammonites belonging to the Phylloceratidae, Tetragonitidae, and Desmoceratidae (Fig. 8).

Septal necks: Because of the short and ambiguous features under a light microscope, we could not observe the detailed morphology of septal necks in the first whorl of most specimens. The septal necks after the second whorl are prochoanitic (=orthochoanitic) in both the Ammonitina and the Lytoceratina, but are amphichoanitic in the Phylloceratina (Fig. 9, Pl. 6). According to the scanning electron micrographs by TANABE *et al.* (*in press*), the septal necks in the first whorl of *E. haradai* and *D. semicostatus* are of prochoanitic type, as shown in Figs. 3, 6 on Pl. 2. DRUSHCHITS *et al.* (1976) reported a thin calcareous layer (termed "cuff" (Манжеты) by them) within or near septal necks in some Upper Paleozoic and Mesozoic ammonites. Furthermore, they (fig. 7a) described that a more or less long cuff is extended from an adapical end of prochoanitic short septal neck to a central part of a chamber in some species of Phylloceratina. However, such a calcareous layer has not been observed in

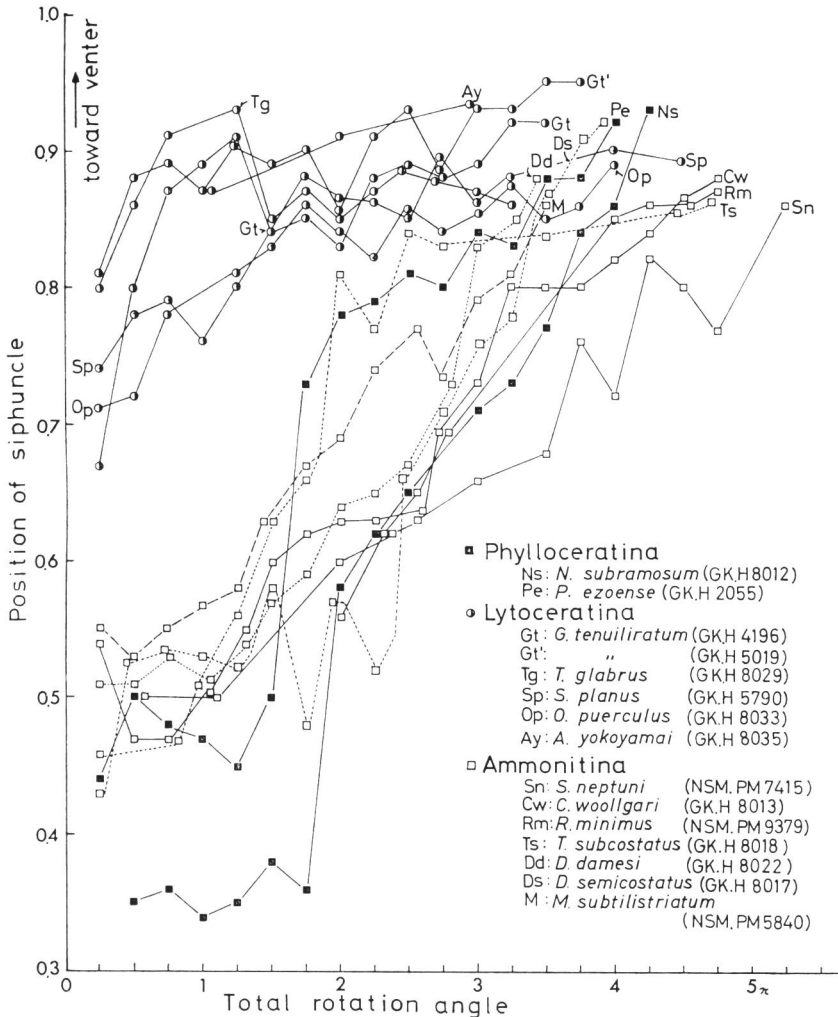


Fig. 7. Ontogenetic change of siphuncle position to total rotation angle of a spiral in selected species. Position of siphuncle is expressed by the parameter shown in Fig. 2.

any specimen examined. Therefore, we interpreted the septal necks of the Cretaceous Phylloceratidae as amphichoanitic, as ZAKHAROV (1974) has already pointed out.

The septal necks are fairly long in the species of *Neophylloceras*, *Phyllopachyceras*, *Damesites*, *Gaudryceras*, *Tetragonites*, and *Polyptychoceras* (for example, they attain about 30% of a chamber length in the fourth-fifth whorls of *D. ainuanus* and *G. tenuiliratum*; Pl. 6, Figs. 3, 11). Conversely, such species as *C. woollgari*, *Y. jimboi*, *K. ishikawai*, *O. puerculus*, and *S. planus* have very short necks throughout the whole stages of ontogeny. It follows that long septal necks are characteristic of the species with

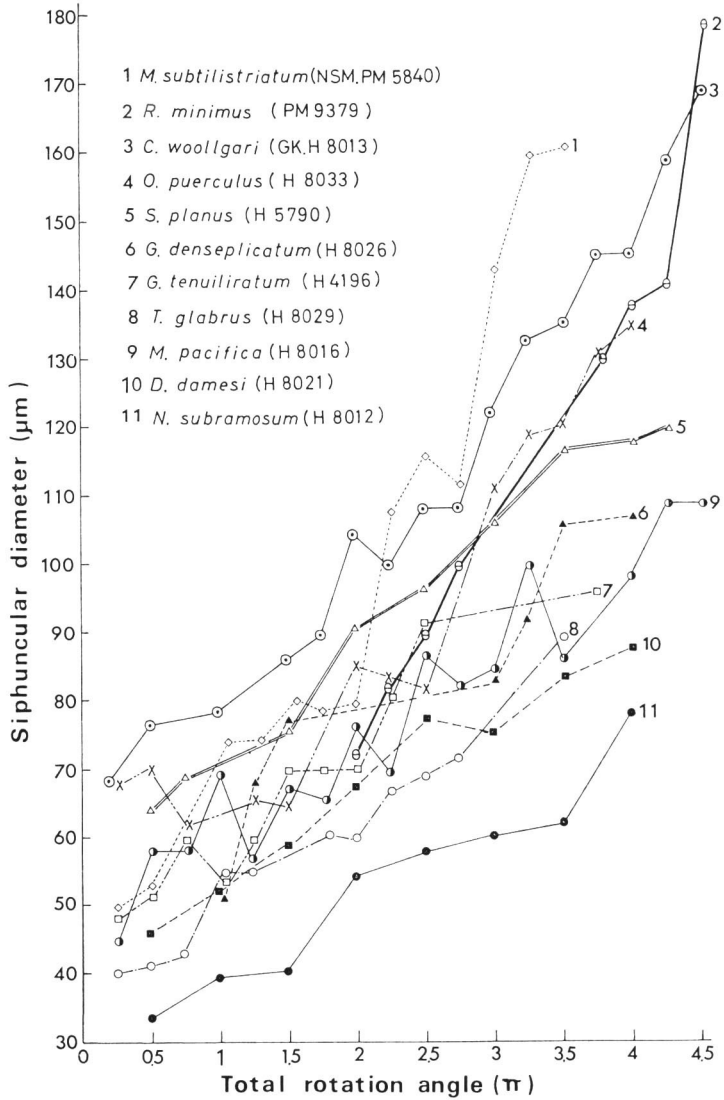


Fig. 8. Growth pattern of siphuncular diameter to total rotation angle of a spiral in selected species.

a narrow siphuncular tube. The ventral side of septal necks in the Lytoceratina is completely enveloped by an outer shell wall, while it is distinctly separated from a ventral wall in every species of Phylloceratina and Ammonitina studied (Fig. 9, Pl. 6).

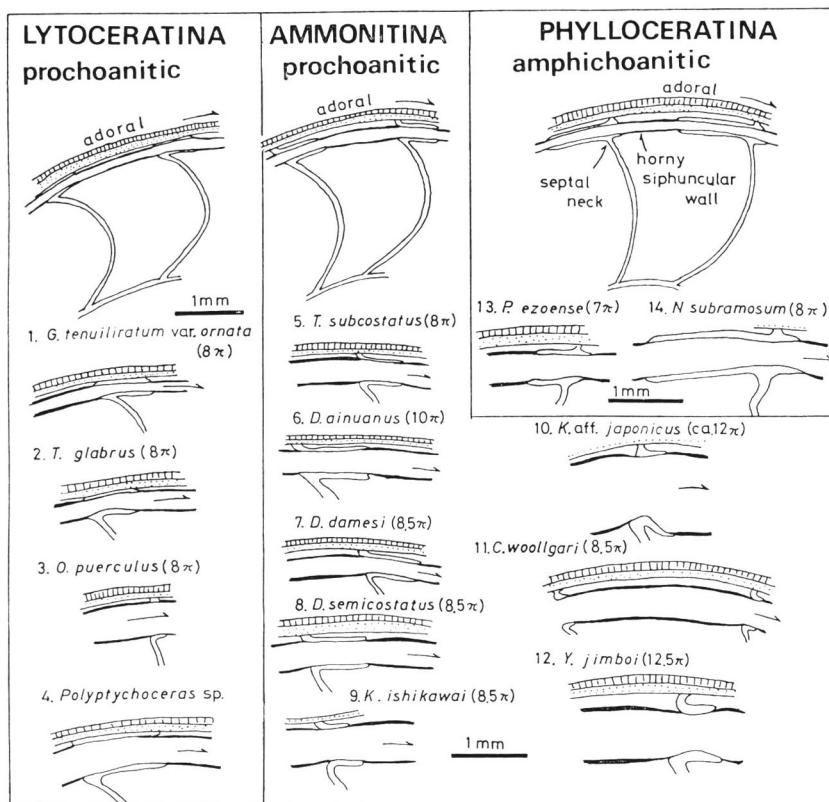


Fig. 9. Drawings showing the morphology of septal neck in selected species. 1. GK. H 8027, 2. H 8029, 3. H 8033, 4. H 8034, 5. H 8018, 6. H 8019, 7. H 8022, 8. H 8017, 9. H 8041, 10. H 8036, 11. H 8013, 12. H 8015, 13. H 2055, 14. H 8011.

Discussion

As described before, the Upper Cretaceous ammonites studied show certain characteristic features for the morphology and ontogeny of internal shell structure in the early stage. We discuss here the results of our observation with respect to major taxonomy. They are concisely summarized in Fig. 10.

In the 28 species examined, the prosiphon is extremely short and adorally convex in the Lytoceratina and the Phylloceratina, whereas it is long and straight in the Ammonitina. A similar fact has already been noticed in some Jurassic and Cretaceous ammonites by SHIMIZU (1929), DRUSHCHITS & KHIAMI (1969, 1970), ZAKHAROV (1974), DRUSHCHITS & DOGUZHAYEVA (1974), and DRUSHCHITS *et al.* (1977a, b). According to GRANDJEAN (1910), in the Middle Jurassic ammonites, *Ludwigia opalina* and *Sphaeroceras brongniarti*, the prosiphon is also very long and straight, as in many Cretaceous

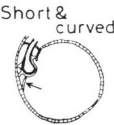

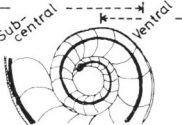
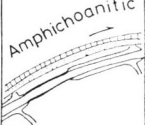
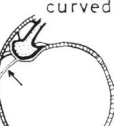

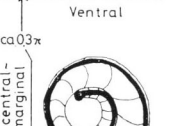

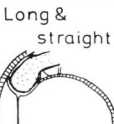

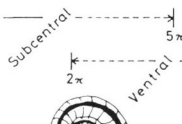

Char- acter Sub- order	Protoconch	Prosiphon	Flange	Caecum	Ammonitella	Position of siphuncle		Septal necks
						0 1 2 3 4 5 π		
Phylloceratina	Medium-sized (0.54-0.66 mm)	Short & curved 	Present	Elliptical or rounded 	Medium-sized (0.90-1.30 mm)	Sub-central 	Amphichoanitic 	
Lytoceratina	Very large (Tetragonitidae, 0.66-1.1 mm) Small (Scaphitidae, 0.35-0.64 mm)	Short & curved 	Absent	Semi-circular 	Very large (Tetragonitidae, 1.34-1.88 mm) Small (Scaphitidae, 0.64-1.1 mm)	Ventral ca 0.3 π Subcentral - marginal 	Prochoanitic 	
Ammonitina	Small (0.38-0.61 mm)	Long & straight 	Absent ex. <i>Reesidites minimus</i>	Elliptical or rounded 	Small (0.74-1.09 mm)	Subcentral 2 π Ventral 5 π 	Prochoanitic 	

Fig. 10. Diagram showing the internal shell structural characteristics in the early stage of Upper Cretaceous ammonites at suborder level. *Adapted from SHIMIZU (1929, pl. 2, fig. 5).

Ammonitina. However, it is extremely short and adorally-convex in two examples of Lower Jurassic Ammonitina, *Arietites kridion* and *Amaltheus margaritatus*, which more closely resemble in this respect Phylloceratina and Lytoceratina than Cretaceous Ammonitina. These facts suggest us that in the Ammonitina the prosiphon may have changed from a short and curved type to a long and straight one during the period of Lower to Middle Jurassic.

From our study on the Upper Cretaceous ammonites, it has been made clear that each suborder has its own characteristic pattern in the ontogenetic change of siphuncle position. Namely, in the Lytoceratina the position changes from subcentral to ventral in the early half of the first whorl, while the marginal approximation is prolonged up to the end of the second whorl or to the middle of the third whorl in the Ammonitina and the Phylloceratina. Similar patterns of ontogenetic change in the siphuncle position in respective suborders have also been confirmed by previous works on many Jurassic and Cretaceous ammonites (BRANCO, 1879-80; SMITH, 1898; GRANDJEAN, 1910; SHIMIZU, 1929; SPATH, 1933; DRUSHCHITS & KHIAMI, 1969, 1970; ZAKHAROV, 1974; DRUSHCHITS & DOGUZHAYEVA, 1974; DRUSHCHITS *et al.*, 1976). This and previous works, thus, suggest that patterns of ontogenetic change in siphuncle position are important to consider the major taxonomy and phylogeny of the Mesozoic

Ammonoidea. According to SPATH (1933, fig. 7), the marginal approach of siphuncle in several Middle Jurassic Ammonitina and Upper Triassic Phylloceratina is attained at the end of the third whorl. Therefore, it seems to be generally certain that the ontogenetic change in siphuncle position in the Ammonitina and the Phylloceratina may have been gradually accelerated with time.

Recently, DRUSHCHITS *et al.* (1976) have demonstrated the general characteristics of siphuncle position in the Ammonoidea. According to them, throughout all stages of ontogeny and phylogeny the siphuncle occupies a dorsal position in the Clymeniina in contrast to a ventral position in the Anarcestina; in the Goniatitina and the Ceratitina the position is unstable up to the third whorl and thereafter ventral. The previous works on the trends of major evolution for the ontogenetic and phylogenetic changes of septal necks by SPATH (1933), BÖHMERS (1936), ZAKHAROV (1974), and DRUSHCHITS *et al.* (1976) are summarized as follows: (1) the Clymeniina and the Anarcestina have retrochoanitic septal necks throughout ontogeny and phylogeny, (2) the ontogenetic transition from retrochoanitic to prochoanitic necks appears in the Goniatitina, Ceratitina, Phylloceratina, and Lytoceratina, (3) the appearance of prochoanitic necks during ontogeny has had been gradually accelerated from the Goniatitina to the Lytoceratina by way of the Ceratitina and the Phylloceratina, and (4) the Ammonitina have prochoanitic necks throughout ontogeny and phylogeny. According to DRUSHCHITS *et al.* (1976), the transition from retrochoanitic to prochoanitic necks in the late Cretaceous tetragonitids belonging to *Gaudryceras* and *Saghalinites* occurs within the first whorl.

We have confirmed the fact (4) in the examined examples of Upper Cretaceous Ammonitina. But the amphichoanitic necks in our observation of the Phylloceratina are inconsistent with the opinion of DRUSHCHITS *et al.* (1976). To solve this problem, further work is required for the microstructure of the connected part in more examples of the Phylloceratina.

Most previous work on ammonoid major taxonomy is based on particular patterns in the ontogenetic development of sutures, morphology of shell form and sculpture, and stratigraphic distribution pattern at low taxonomic levels. As shown in Fig. 10, the results of this work essentially support the scheme of the major taxonomy of the Cretaceous Ammonoidea distinctly proposed by ARKELL *et al.* (1957) and DRUSHCHITS *et al.* (1958). Opinions, however, remain divided as to the major taxonomic position of the Scaphitidae. MIKHAILOV & DRUSHCHITS (1958), and DRUSHCHITS & DOGUZHAYEVA (1976) attributed the family to the Ammonitina, because of the ontogenetic suture development and the prochoanitic septal necks in all stages of ontogeny. Conversely, WRIGHT (1953), ARKELL *et al.* (1954), and WESTERMANN (1971) included it into the Lytoceratina, relying on the characteristics of adult sutures and the presence of a dorsal shell wall. It has been revealed from this work that with respect to the internal shell structure of examined examples, the Scaphitidae are more closely similar to the Tetragonitidae than the Ammonitina, especially concerning the shape of prosiphon, completely enveloped septal necks and ontogenetic change in

siphuncle position. This fact suggests that the Scaphitidae should be included in the Lytoceratina rather than the Ammonitina.

Although the morphologic characters of such structural elements as protoconch, partial septa, caecum, flange, and ammonitella are stable within species belonging to several families, their intra- and/or interspecific variation is fairly large as compared with the prosiphon, septal necks, and siphuncle. To evaluate the taxonomic implications of these elements, we should further examine the inter- and intraspecific variation in large samples of many species.

Summary

The characteristics of the internal shell structure in the early growth-stage of the 28 species of Upper Cretaceous ammonites (2 Phylloceratina, 17 Ammonitina, and 9 Lytoceratina) have been described with many well-preserved polished and thin sectioned specimens from Hokkaido and South Sakhalin. Certain patterns in the shape of prosiphon, morphology of septal necks, and ontogenetic change in siphuncle position, are commonly recognized among the examined species of the same suborder, and each suborder has its own characteristics in these early internal characters. We have also described such characters as form and structure of partial septa and caecum, protoconch and ammonitella sizes, position of nepionic constriction, and ontogenetic growth pattern of siphuncular diameter in each species. We have, furthermore, discussed the implications of the observed facts to major taxonomy.

It is suggested that the study of ontogenetic development of internal shell structures is as much important as that of suture, shape and sculpture of shells to construct the adequate scheme of major taxonomy and phylogeny of the Cretaceous Ammonoidea.

Acknowledgements. We thank Professor Emeritus T. MATSUMOTO of Kyushu University for his valuable suggestions and critical reading of the manuscript. We are also indebted to Dr. I. HAYAMI, Professors T. BIRKELUND and J. WIEDMANN, and Dr. C. W. WRIGHT for their useful discussions. Financial aid was granted from the Science Research Fund of the Japanese Ministry of Education, Science and Culture (OBATA, no. 254267 for 1977, TANABE, no. 374257 for 1978, and TAKAYANAGI, no. 334043 (Grant-in-Aid for Co-operative Research) for 1978–79).

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Note added in proof. KULLMANN & WIEDMANN (1970) included all of the Mesozoic heteromorphs in the single suborder, Ancyloceratina, because of their characteristic quadrilobate primary suture, expressed as ELUI in terms of WEDEKIND's formula. They interpreted that the quadrilobate primary suture in the heteromorphs may reflect a monophyletic origin, at least for the Ancylocerataceae and the Turrititaceae. In September of 1979, one of us (K. T.) visited at the Universität Tübingen to study the well-preserved specimens with protoconch of the Berriasian heteromorph *Leptoceras studeri* (OOSTER) and the Lower Barremian douvilleiceratid *Paraspitoceras schindewolfi* WIEDMANN, both of which were illustrated by WIEDMANN (1969, pl. 3, fig. 1 and pl. 2, fig. 1). However, he could not observe the siphuncle position in the initial stage of the specimens. At present, we can not mention about the major taxonomic position of the Cretaceous heteromorphs from the viewpoint of early ontogeny of internal structure, owing to the insufficient data on this problem. We thank Prof. J. WIEDMANN who has given us a permission to examine the type collection in his care.

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Explanation of Plates

Plate 1

Figs. 1–8. Light (1–3, 6–8) and scanning electron (4–5) micrographs of early internal shell structure in selected species.

Fig. 1. *Neophylloceras subramosum*. GK. H 8012. $\times 120$.

Fig. 2. *Gaudryceras tenuiliratum*. GK. H 4196. $\times 120$.

Fig. 3. *Otoscaphtes puerculus*. GK. H 8033. $\times 100$.

Fig. 4. *Damesites semicostatus*. GK. H 8039. $\times 115$.

Fig. 5. *Eupachydiscus haradai*. GK. H 8024. $\times 100$.

Fig. 6. *Damesites damesi*. GK. H 8023. $\times 120$. Arrow points to branch of prosiphon.

Fig. 7. *Damesites semicostatus*. GK. H 8017. $\times 120$.

Fig. 8. *Mesopuzosia pacifica*. GK. H 8016. $\times 120$.

Photos by TANABE (1–3, 6–8) and FUKUDA (4–5).

Plate 2

Figs. 1–2, 6. Scanning electron micrographs of prosiphon (1), caecum (2), and septal neck at 0.5π stage (6) in *Damesites semicostatus*. GK. H 8039. 1($\times 4800$), 2($\times 2000$), 6($\times 500$). psh: prosiphon.

Figs. 3–4, 5. Scanning electron micrographs of prosiphon (4), caecum (5), and septal neck at 0.5π stage (3) in *Eupachydiscus haradai*. GK. H 8024. 3($\times 360$), 4($\times 2000$), 5($\times 1400$). Psh: prosiphon.

Arrow in Figs. 3 and 6 shows the adoral direction. Scale (μ means μm) and acceleration voltage are indicated in each figure.

Photos by FUKUDA.

Plate 3

Figs. 1–6. Light micrographs showing the ontogenetic change of siphuncle position in selected Lytoceratina (all $\times 20$).

Fig. 1. *Tetragonites glabrus*. GK. H 8029.

Fig. 2. *Gaudryceras tenuiliratum*. GK. H 4190.

Fig. 3. *Gaudryceras tenuiliratum* (var. *ornata*). GK. H 8027.

Fig. 4. *Gaudryceras denseplicatum*. GK. H 8026.

Fig. 5. *Otoscaphtes puerculus*. GK. H 8033.

Fig. 6. *Scaphites planus*. GK. H 5790.

Photos by TANABE.

Plate 4

Figs. 1–6. Light micrographs showing the ontogenetic change of siphuncle position in selected Ammonitina (all $\times 20$).

Fig. 1. *Damesites damesi*. GK. H 8020.

Fig. 2. *Damesites damesi*. GK. H 8021.

Fig. 3. *Damesites semicostatus*. GK. H 8017.

Fig. 4. *Mesopuzosia pacifica*. GK. H 8016.

Fig. 5. *Kitchinites ishikawai*. GK. H 8015.

Fig. 6. *Hauericeras gardeni*. GK. H 8025.

Photos by TANABE.

Plate 5

Figs. 1–5. Light (1–2, 4–5) and scanning electron (3) micrographs showing the ontogenetic change of siphuncle position in selected Ammonitina and Phylloceratina.

- Fig. 1. *Collignonicerias woollgari*. GK. H 8013. $\times 20$.
 Fig. 2. *Metaplacenticeras subtilistriatum*. NSM. PM 5840. $\times 20$.
 Fig. 3. *Eupachydiscus haradai*. GK. H 8024. $\times 30$.
 Fig. 4. *Neophylloceras subramosum*. GK. H 8012. $\times 20$.
 Fig. 5. *Phyllopachyceras ezoense*. GK. H 2055. $\times 20$.
 Photos by TANABE (1–2, 4–5) and FUKUDA (3).

Plate 6

Figs. 1–13. Light micrographs showing the morphology of median sectioned septal necks in selected species (all $\times 20$). Arrow means the adoral direction.

- Fig. 1. *Tragodesmocerooides subcostatus*. GK. H. 8018. 8π stage.
 Fig. 2. *Damesites damesi*. GK. H 8022. 8.5π stage.
 Fig. 3. *Damesites ainuanus*. GK. H 8019. 10π stage.
 Fig. 4. *Damesites semicostatus*. GK. H 8017. 8.5π stage.
 Fig. 5. *Mesopuzosia yubarensis*. GK. H 8040. 10π stage.
 Figs. 6–7. *Kitchinites ishikawai*. GK. H 8041 (6) 9.5π stage, GK. H 8015(7) 8π stage.
 Fig. 8. *Polyptychoceras* sp. GK. H 8034. At 6 mm in whorl height.
 Fig. 9. *Yokoyamaoceras jimboi*. GK. H 8014. 12.5π stage.
 Fig. 10. *Collignonicerias woollgari*. GK. H 8013. 9π stage.
 Fig. 11. *Gaudryceras tenuiliratum* var. *ornata*. GK. H 8027. 8π stage.
 Fig. 12. *Tetragonites glabrus*. GK. H 8029. 8π stage.
 Fig. 13. *Neophylloceras subramosum*. GK. H 8011. 8.5π stage.

Photos by TANABE.

