Ontogenetic Development and Functional Morphology in the Early Growth-Stages of Three Cretaceous Ammonites*

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Introduction

Recent electron microscope studies on ammonoid shell microstructure have greatly contributed to clarify the early ontogenetic development of the group. Such authors as BIRKELUND (1967), BIRKELUND & HANSEN (1968, 1974), ERBEN et al. (1968, 1969), DRUSHCHITS & KHIAMI (1969, 1970), ERBEN & REID (1971), and DRUSHCHITS et al. (1977a, b) have made clear that a definite pattern for the ontogenetic development of shell wall, septa, and septal necks occurs in the early growth-stages of many ammonoids.

The microstructural characteristics of prosiphon, caecum, partial "septa" etc., however, have not yet been fully described, although they may be important to consider the early ontogeny and functional morphology of the Ammonoidea. As TANABE et al. (1979) have already pointed out, the late Cretaceous ammonites from the meridional zone of Hokkaido are so well preserved in calcareous nodules that they may be suitable for the study of early ontogenetic development. In this article, we discuss the ontogenetic development and functional morphology in the early stage of the three Cretaceous ammonites through the SEM investigations of internal shell microstructure on several well-preserved specimens from the region.

Material

This work is based on four well-preserved specimens of *Mesopuzosia yubarensis*

(Jimbo), *Damesites semicostatus* Matsumoto, and *Eupachydiscus haradai* (Jimbo), as recorded below with their locations and horizons.

M. yubarensis: One specimen (GK. H 8038) from a nodule lay in the Sekitannaizawa, the tributary of the Shimokinembets River, Obira area, northwestern Hokkaido. Middle Turonian.   K. Tanabe coll.

D. semicostatus: Two specimens (GK. H 8039, 8085) from a nodule in mudstone beds at loc. R 2673 in the middle stream of the Jugosenzawa, the tributary of the Obirashibe River, Obira area.   Lower Santonian.   H. Hirano & K. Tanabe coll.

E. haradai: One specimen (GK. H 8024) from a nodule lay in the middle stream of the Abeshinai River, Saku area, northern-central Hokkaido.   Lower Campanian. K. Tanabe coll.

The specimens utilized are deposited at Kyushu University with the registered number shown in parentheses.   According to Arkell *et al.* (1957), these three species belong to the suborder Ammonitina.

Preparation

For the SEM observation of internal structure, each specimen was first cut or polished along the median dorsoventral plane.   The median-sectioned specimen was etched with 4% hydrochloric acid for about three minutes, and subsequently the etched specimen was washed with pure water for several times.   The etched surface was coated with gold or carbon for ten minutes using an ioncoater (Eiko Engineering Co., IB-3 type).   The microstructural observation was made on the carbon- or gold-coated median plane by means of a scanning electron microscope (SEM) (Hitachi Co., H-450 type) of the Chiba Prefectural Institute of Public Health under 20KV for an acceleration voltage.   We also analysed the ultimate composition of several structural elements on the carbon-coated specimen of *D. semicostatus* (GK. H 8085) with an aid of an energy dispersive X-ray microanalyser (EDX) (Kevex Co., 7000 type) attached to the SEM.

Internal Structural Characteristics of Ammonitella

Before describing the shell microstructure, we briefly summarize the internal structural characteristics of ammonitella.   The term ammonitella was defined as a conch with a nepionic constriction (=primary varimax used by Russian paleontologists) at its aperture by Drushchits & Khiami (1969).   As diagrammatically illustrated in Fig. 1, the ammonitella of all ammonoids consists of such internal structural elements as protoconch, prosiphon, caecum, prosepta, siphuncle, septa, septal necks, and shell wall with a nepionic constriction (Branco, 1879–80; Grandjean, 1910; Spath, 1933; Böhmers, 1936; Miller & Unklesbay, 1943; Erben *et al.*, 1969; Zakharov, 1974; Drushchits & Doguzhayeva, 1974; Tanabe *et al.*, 1979).   Some ammonoids also have partial "septa" (termed by Shimizu, 1929, but they are structurally similar to

prosiphon rather than septa) and flange in the ammonitella, but the three species examined do not possess these characters (*see* Pl. 1). As will be discussed after the description, septa, septal necks, and majority of siphuncle in the ammonitella were probably secreted after the formation of the nepionic constriction. DRUSHCHITS & DOGUZHAYEVA (1974), ZAKHAROV (1974), and TANABE *et al.* (1979) have noticed the fact that ammonoids have their own characteristic features in the above-mentioned early internal structures at superfamily or suborder level.
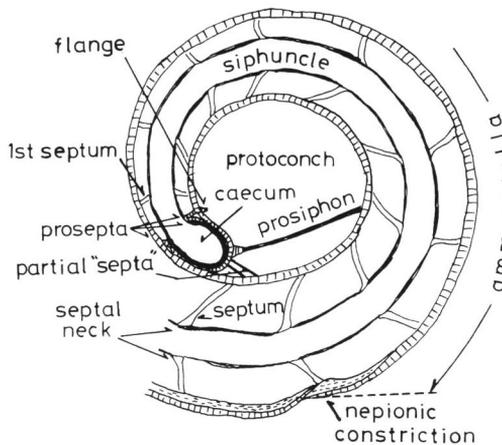

Fig. 1. Diagram showing the internal structural characteristics of the ammonitella in the median section. Terminologies are cited from BRANCO (1879–80), GRANDJEAN (1910), SHIMIZU (1929), and DRUSHCHITS & KHIAMI (1969).

Description of Microstructure

Protoconch wall: The microstructure of protoconch wall is well preserved in GK. H 8024 of *E. haradai*. The SEM micrographs of the portion (Figs. 1–2 on Pl. 2) show that the protoconch wall is composed of a thin subprismatic layer of about 5 μm in thickness. In the ventral part near the caecum the inner part of the layer consists of elongate crystals which are arranged at right angle to the inner surface; the crystals of the outer part, however, do not show any apparent orientation (*see* Fig. 1 on Pl. 2). ERBEN *et al.* (1969) distinguished three subprismatic sublayers within the protoconch wall in some ammonoids, and discussed their ontogenetic development. Such sublayers, however, are not ascertained in the specimens examined. As shown in Figs. 1–4 on Pl. 1, Fig. 1 on Pl. 3, and Fig. 2, in the three species examined the protoconch wall is directly linked with the succeeding prosepta and outer calcareous layer of caecum without any trace of adapical extension, flange.

Prosiphon: All of *E. haradai*, *M. yubarensis*, and *D. semicostatus* have a long, nearly straight prosiphon whose morphology is one of the characteristic features in

the Cretaceous Ammonitina (TANABE *et al.*, 1979).   In the examined specimens of *E. haradai* and *D. semicostatus* it is extended from the posterior part of protoconch wall to the adapical part of caecum (*see* Figs. 1–3 on Pl. 1).   The prosiphon could not be observed in GK. H 8038 of *M. yubarensis*, because of inexact cutting along the median plane.   As the prosiphon in GK. H 8039 of *D. semicostatus* happened to be partly broken in the central part, we can observe the internal structure of prosiphonal wall in detail.   The SEM micrograph of the portion (Fig. 3 on Pl. 3) shows that the pro-siphon is a fine tube of about 5 μm in diameter.   The wall, about 1 μm thick, is charac-terized by the multi-layered structure of compact material.   The layered microstructure of prosiphonal wall is closely similar to that of a chitinous siphuncular wall in am-monites and that of inner horny membranes of siphuncular wall in modern *Nautilus* (Fig. 1 on Pl. 5; MUTVEI, 1972; OBATA *et al.*, *in prep.*).

The similar microstructural features of a prosiphonal wall are also observed in GK. H 8024 of *E. haradai*.   As shown in Fig. 3 on Pl. 1 and Fig. 5 on Pl. 3, the prosi-phon tends to be larger toward caecum, and at the base of caecum it attains to about 30 μm in diameter.   The enlarged SEM micrograph around the caecum (Fig. 6 on Pl. 3) shows that the prosiphonal wall is formed of multi-layered organic membranes with a thin calcareous covering (about 1 μm thick) which is apparently connected with the outer calcareous layer of caecum wall (*see* also Fig. 5 on Pl. 3).

From these observations it seems certain that the prosiphonal tube is directly connected with the inner horny layer of caecum wall.   As to be described later, the inner horny layer of caecum wall is the initial part of siphuncular tube.   This means that a prosiphonal tube is equivalent to a siphuncular tube in form and microstructure.

To determine the mineral composition of a prosiphonal wall, we made the EDX analysis on GK. H 8035 of *D. semicostatus*.   As shown in the characteristic X-ray images of silica and calcium on the part of carbon-coated median sectioned specimen (Figs. 2–3 on Pl. 5), the aragonitic shelly parts such as shell wall and septa had been diagenetically replaced by silica-rich material, but a large amount of phosphate along the prosiphonal wall was recognized by the line EDX analysis (Fig. 3).   According to OBATA *et al.* (*in prep.*), the siphuncular wall in the specimen of *Scalarites scalaris* (YABE) from the Obira area is also rich in phosphate.   Although we were unable to decide directly the original mineral composition of prosiphonal wall, the structural relationship between prosiphon and siphuncle and the line EDX analysis suggest that the original composition of prosiphonal wall is probably chitinous, like that of the siphuncular wall.

Caecum wall: The three species examined have a round or elliptical caecum which is convex adapically in the median section (Pl. 1).   The caecum wall in the three species consists of an outer, thinner calcareous layer and an inner, thicker horny layer (Figs. 1–2, 4, 7 on Pl. 3; Figs. 1–2 on Pl. 4).   The outer layer, about 3 μm in every species, is founded up of closely packed calcareous crystals in which no apparent layered structure is observed.   As shown in Fig. 4 on Pl. 3, in *M. yubarensis* the outer (adapical) surface of caecum wall is smooth without any trace of surface ornamen-
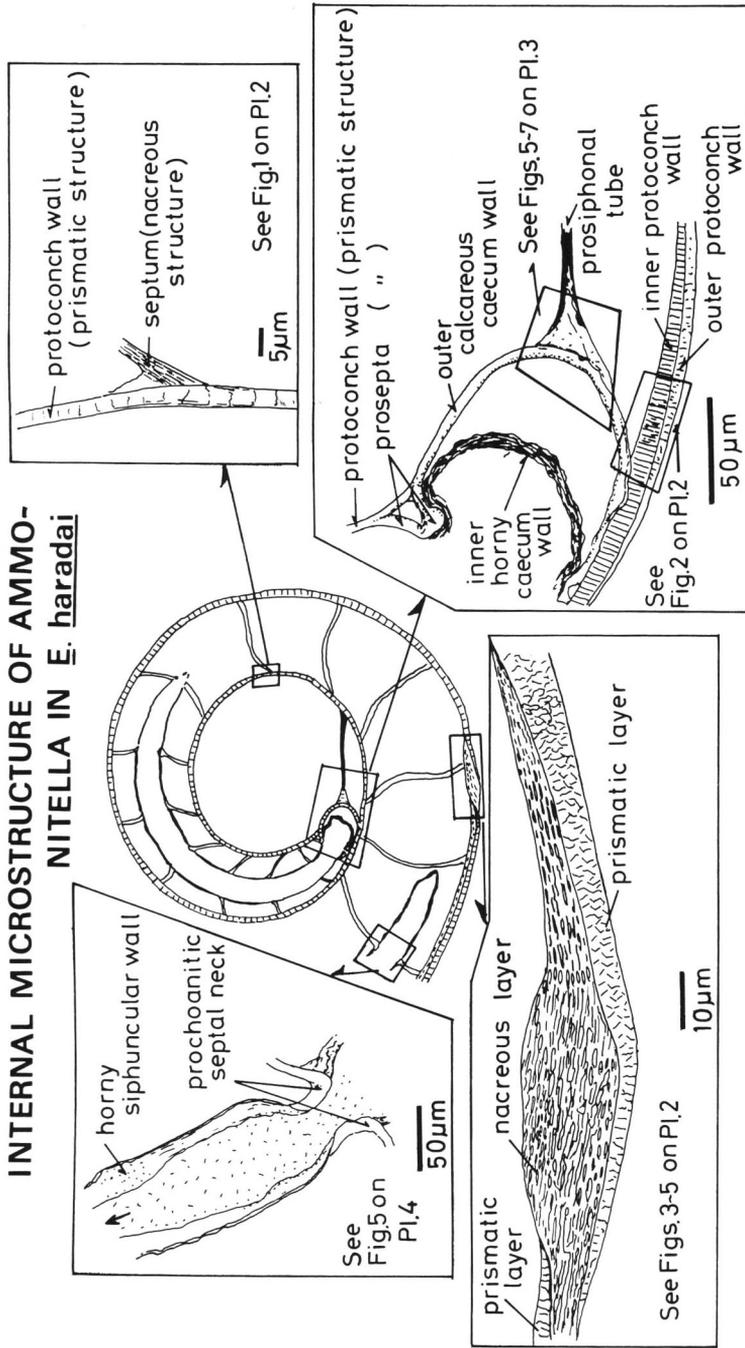
INTERNAL MICROSTRUCTURE OF AMMO-
NITELLA IN E. haradai

protoconch wall (prismatic structure)
septum (nacreous structure)
See Fig.1 on Pl.2
5μm

protoconch wall (prismatic structure)
prosepta (")
outer calcareous caecum wall
See Figs.5-7 on Pl.3
prosiphonal tube
inner protoconch wall
outer protoconch wall
inner horny caecum wall
See Fig.2 on Pl.2
50μm

horny siphuncular wall
prochoanitic septal neck
See Fig.5 on Pl.4
50μm

prismatic layer
nacreous layer
prismatic layer
prismatic layer
See Figs.3-5 on Pl.2
10μm

Fig. 2. Drawings of the microscopic features of selected parts of the ammonitella in GK. H 8024 of *Eupachydiscus haradai*.
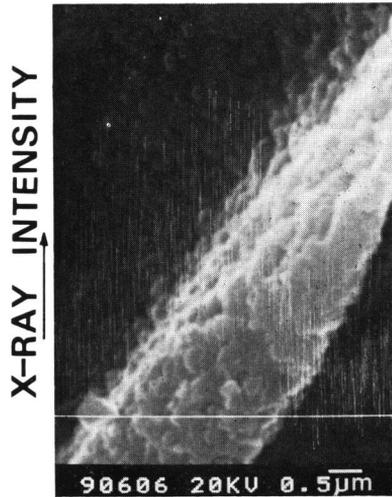
Fig. 3. Characteristic X-ray intensity spectrum of phosphate along prosiphonal wall on GK. H 8085 of *Damesites semicostatus.*   ×1400.

tation, as in the Upper Jurassic *Xipheroceras ziphus* (Erben *et al.*, 1969, fig. 6 on pl. 4) and *Pavlovia* sp. (Erben & Reid, 1971, fig. 4 on pl. 1).   In *E. haradai* and *D. semicostatus* the dorsal extension of this layer is directly linked with the two prosepta (Fig. 1 on Pl. 3; Fig. 2).   Erben & Reid (1971) reported the same relationship between the outer caecum layer and the proseptum in *Pavlovia* sp.

The inner layer of caecum wall is directly covered with the outer one in GK. H 8085 of *D. semicostatus* (*see* Fig. 1 on Pl. 1), although it has been secondarily segregated from the outer one in the other specimens examined (Figs. 2–4 on Pl. 1).   As shown in Figs. 1–4 on Pl. 1, the inner layer corresponds to the initial part of the succeeding siphuncular wall.   In *D. semicostatus* and *E. haradai* it is characterized by the multi-layered microstructure of horny material, as in the siphuncular wall (Fig. 1 on Pl. 3; Figs. 1–2 on Pl. 4).

Prosepta: *E. haradai* and *D. semicostatus* have two short prosepta at the constricted base of caecum (Fig. 1 on Pl. 3; Fig. 2).   In both species their length in the dorsal side (ca. 20 μm) is much longer than that in the ventral one (ca. 10 μm).   The first proseptum obviously corresponds to an adoral extension of the outer calcareous layer of caecum wall, and it is connected with the second proseptum at the base of caecum.   The second proseptum is gently convex toward the apex in constrast to the adorally convexed succeeding septa.   We were unable to observe the microstructure of prosepta in the specimens examined.   Erben *et al.* (1969) described prismatic prosepta in some Paleozoic and Mesozoic ammonoids.   Judging from the intimate structural relationship among protoconch wall, outer caecum wall, and prosepta, it is suggested that both *E. haradai* and *D. semicostatus* have also prismatic prosepta.

Septa and septal necks: As shown on Pl. 1, the ammonitella in the specimens examined has 9 (*D. semicostatus* and *M. yubarensis*) or 11 (*E. haradai*) regular-spaced septa which are gently convex adorally. The 8th septum in GK. H 8024 of *E. haradai* is composed of multi-layered tabular aragonitic crystals which are arranged in parallel to the outer and inner septal surfaces (Fig. 1 on Pl. 2; Fig. 2). This observation suggests us that septa in the three species examined are constructed from the nacreous layer, as in many ammonoids studied by BIRKELUND (1967), BIRKELUND & HANSEN (1968, 1974), ERBEN *et al.* (1969), ERBEN & REID (1971), and KULICKI (1979).

The three species examined have short, prochoanitic (prosiphonate) septal necks in the early-growth stages (Figs. 3, 5 and 6 on Pl. 4). In *D. semicostatus* the necks tend to be longer after the second whorl (Fig. 4 on Pl. 4).

Recently, BANDEL & BOLETZKY (1979) have summarized the morphologic characteristics of ammonoid septal necks, following the previous works of BRANCO (1880), BÖHMERS (1936), ERBEN & REID (1971), and BAYER (1975). According to their diagram (fig. 26), septal necks in ammonoids are formed of such structural elements as the nacreous layer, porous prismatic zone, and de-coupling room; and the horny siphuncular tube does not exist around the septal necks. Although we could not confirm the existence of decoupling room and porous prismatic zone in the specimens examined under the SEM, the siphuncular tube is not continuous at the site of septal neck even in the early stage (Figs. 3, 5, and 6 on Pl. 4; Fig. 2).

Shell wall: Based on the well-preserved specimen, GK. H 8024, of *E. haradai*, we made the SEM observation on the shell wall microstructure in the first whorl. The ventral shell wall in most stages of the first whorl of the specimen is made up of the prismatic layer (Fig. 3a on Pl. 2). It starts from the inner prismatic sublayer of protoconch wall near the ventral side of caecum (Fig. 2 on Pl. 2) and gradually becomes thicker with growth. Its thickness attains to the maximum (10 μm) immediately before the nepionic constriction. BIRKELUND (1967, fig. 4 on pl. 2) distinguished an outer sublayer with crystals of random orientation within the ventral shell wall of the first whorl in the late Cretaceous *Saghalinites wrighti* from Greenland. Such an outer sublayer, however, was not observed in the specimens examined (*see* Fig. 3 on Pl. 2).

Nepionic constriction: The three species examined have a clear nepionic constriction near the end of the first whorl (Pl. 1) Figs. 3–5 on Pl. 2 are the SEM micrographs showing the microstructure of shell wall around the nepionic constriction in GK. H 8024 of *E. haradai*. At the stage of about 320° in total rotation angle from the centre of protoconch, a thin nacreous layer begins to appear on the inner side of the preceding prismatic layer (Fig. 3a on Pl. 2). It gradually thickens with growth, and attains to the maximum thickness (ca. 20 μm) at the nepionic constriction. Subsequently, both inner nacreous and outer prismatic layers forming the nepionic constriction abruptly decrease their thickness with growth, and at the end of the constriction they are replaced by a new set of outer prismatic and inner nacreous layers (*see* Fig. 2). Fig. 3b on Pl. 2 shows the transitional part from the inner nacreous layer forming the constric-

tion to the newly secreted outer prismatic layer of the second whorl. As given in Figs. 4–5 on Pl. 2, the inner nacreous layer is composed of alternating tabular aragonite crystals and organic sheets which are arranged in parallel to the outer shell surface. The size of aragonite crystals remains constant at every part with 3 to 5 μm in width and less than 1 μm in thickness.

The above-mentioned remarkable changes in shell microstructure at the nepionic constriction have already recognized in many ammonoids (BIRKELUND, 1967; BIRKELUND & HANSEN, 1968, 1974; ERBEN, 1962, 1964; ERBEN et al., 1969; ERBEN & REID, 1971; DRUSHCHITS & KHIAMI, 1970; DRUSHCHITS & DOGUZHAYEVA, 1974; HIRANO, 1975; DRUSHCHITS et al., 1977b; TANABE et al., 1979; KULICKI, 1979).

Discussions

Ontogenetic development of internal shell structure: As described above, the internal structure of the ammonitella in the three species examined is characterized by such common elements as a protoconch wall, prosiphonal tube, caecum wall, prosepta, septa, siphuncular tube, and shell wall with a nepionic constriction at its aperture. In the specimens of *D. semicostatus* and *E. haradai* the inner layer of caecum wall and the prosiphonal tube are composed of multi-layered organic membranes, while the protoconch wall, outer layer of caecum wall, prosepta, and shell wall immediately before the nepionic constriction are all made up of calcareous material showing the prismatic structure. The nacreous layer first appears in the first septum and the outer shell wall near the nepionic constriction.

Several authors have discussed on the mineral composition of organic structural elements in the early growth-stages of ammonoids. SHIMIZU (1929) interpreted that the dark-coloured prosiphon and inner layer of caecum wall in some well-preserved ammonite specimens from Hokkaido and Sakhalin are composed of calcium phosphate. He also distinguished a thin calcite covering on the inner organic layer of caecum wall and on the prosiphon near the caecum. Formerly, ERBEN (1962) supposed the mineral composition of prosiphon in a specimen of the Cretaceous *Euhoplites tuberculatus* from England as carbonate material only. Thereafter, ERBEN et al. (1969) and ERBEN & REID (1971) modified ERBEN's (1962) opinion to that blackish membranes of a prosiphon in many ammonoids are formed of horny material (conchiolin?).

As to the mineral composition of caecum wall, the observations of ERBEN (1962) and ERBEN & REID (1971) greatly differ from that of SHIMIZU (1929) mentioned above. They regarded that the caecum wall in two specimens of *E. tuberculatus* and *Pavlovia* sp. consists only of conchiolin membranes with a lustrous surface. Our SEM and EDX observations on the microstructure and ultimate composition of prosiphonal and caecum walls in the three Cretaceous ammonites seem to support SHIMIZU's (1929) interpretation. In all probability, the multi-layered membranes of the prosiphonal wall and inner layer of caecum wall in the specimens examined are composed of phosphate-rich material such as calcium phosphate or carbonate apatite which may be a

diagenetic replacement of chitinous material.

As mentioned before, it has been well known that all ammonoids have a nepionic constriction around the end of the first whorl. SMITH (1901) and TRUEMAN (1940) respectively reported very young shells of *Baculites* and *Arnicoeras* which are similar to each other at the ammonitella stage. The shells described by them have a nepionic constriction at their aperture, and the first whorl is septated into only a few chambers. KULICKI (1974, 1975) has suggested that in the Middle Jurassic genus *Quenstedtoceras* a newly hatched animal may have had three complete chambers (protoconch, a chamber septated by two prosepta, and a succeeding body chamber). ERBEN *et al.* (1969) discussed the ontogenetic development of prosepta and septa in the Ammonoidea on the basis of the SEM observation on many well-preserved specimens of about 40 species. According to their model (fig. 5-IV), the first septum was secreted after the completion of the nepionic constriction, because the microstructure of prosepta is prismatic in contrast to the nacreous structure of the first septum. These works suggest us that the specimens examined had no septum and only a very short siphuncle before the secretion of the nepionic constriction.

The results of our observation on the three Cretaceous ammonites may lead to the following successive growth-stages in the early ontogenetic development of the Ammonoidea.

Pre-ammonitella and ammonitella stages (=embryonic stage)

1st substage: A tissue secretes a subprismatic protoconch wall.

2nd substage: The very young body filling the protoconch gradually shifts toward the outside of protoconch, and simultaneously elastic organic membranes of a prosiphonal tube begins to appear. An epithelium of the withdrawing young body secretes a new prismatic layer on the foregoing protoconch wall. The layer grows spirally to form an initial shell of the first whorl.

3rd substage: The prosiphonal tube changes to a cup-shape at the adoral end as the withdrawing of the body goes on, and at this part the organic membranes gradually thicken to become an inner organic layer of a caecum wall. At this substage the first prismatic proseptum is secreted on the successively growing shell wall of the first whorl. The organic membranes on the first proseptum are probably elastic. In some ammonoids the protoconch wall is extended adapically to form a flange.

4th substage: An adapical extension of the protoconch wall covers the preceeding organic membranes of caecum wall, and it becomes to an outer calcareous layer of caecum wall. Therefore, the shell at this substage is distinctly partitioned into the first chamber (protoconch) and the subsequent body chamber by the caecum wall.

5th substage: This substage corresponds to the ammonitella stage. At the beginning of this substage a second proseptum is secreted. Subsequently, a nacreous layer begins to appear on the inner side of the prismatic layer of the shell wall at the end of the first whorl. The nacreous layer abruptly thickens at the final of this substage to form a nepionic constriction. Simultaneously, a nacreous first septum is

secreted.   A part of the siphuncle is formed at this substage.

Post-ammonitella stage (=post-embryonic stage)

A new set of inner nacreous and outer prismatic layers of the second whorl begins to appear after the nepionic constriction.   The soft animal body gradually moves anteriorly forming the shell wall of the second whorl and several septa.

The above-mentioned successive growth-stages are diagrammatically shown in Fig. 4 (A–E).

Ammonoid early ontogeny: There are two different opinions about the early ontogenetic development of the Ammonoidea.   One is represented by MAKOWSKI (1971), ERBEN (1962, 1964, 1966), and ERBEN *et al.* (1968, 1969), who emphasize the metamorphosis.   According to ERBEN *et al.* (*op. cit.*), at the earlist stage the embryonic shell marks a bowl-shaped protoconch.   The embryo secretes one complete whorl at this stage.   In the next stage represented by the successive formation of flange, proseptum, and secondary wall of embryonic shell, the animal is a free swimming veliger or veliger-like larva.   The nepionic constriction is formed at the phase of metamorphosis from larval to post-larval stages.

The other view is that ammonoids developed directly (SHIMANSKIY, 1954; DRUSH-CHITS, 1956; BIRKELUND & HANSEN, 1968, 1974; DRUSHCHITS & KHIAMI, 1969, 1970; KULICKI, 1974, 1975, 1979; DRUSHCHITS *et al.*, 1977b).   According to this theory, there are only two growth-stages, namely embryonic and post-embryonic stages, in the ammonoid ontogenetic development.   KULICKI (*op. cit.*) summarized the early ontogeny of ammonoids as follows: thus such characters as cap-shaped protoconch wall, flange, prosepta, prosiphon, caecum, and shell wall of the first whorl are formed in the egg capsule.   The transition from embryonic to post-embryonic stages is completed after the formation of the nepionic constriction.

It is very difficult to decide whether ammonoids developed directly without a larval stage or not, because ammonoids had been extinct at the end of the Cretaceous Period. Recent works on modern cephalopod early ontogeny, however, may give an important information on this problem.   It has been well known that all modern coleoids do not have a larval stage (BOLETZKY, 1974).   BANDEL & BOLETZKY (1979) have recently made clear the structure, ontogenetic development and morphologic relationships of modern chambered cephalopods in the early stage, comparing them with fossil cephalopods such as the Ammonoidea, Nautiloidea, and Belemnoidea.   According to them, the early shell of *Spirula* closely resembles that of ammonoids in the presence of the first prismatic apertural constriction (proseptum) and the beginning of the siphuncular tube (caecum) with its sheet-like extension (prosiphon) that is fixed to the protoconch wall (*cf.* their figs. 5, 64–69).   They also mentioned that the shape and composition of the early shell of *Spirula* are essentially similar to those of the Belemnoidea, whereas these characters are quite different from those of *Sepia* and nautiloids. From these observations they concluded that the similarity of early internal shell
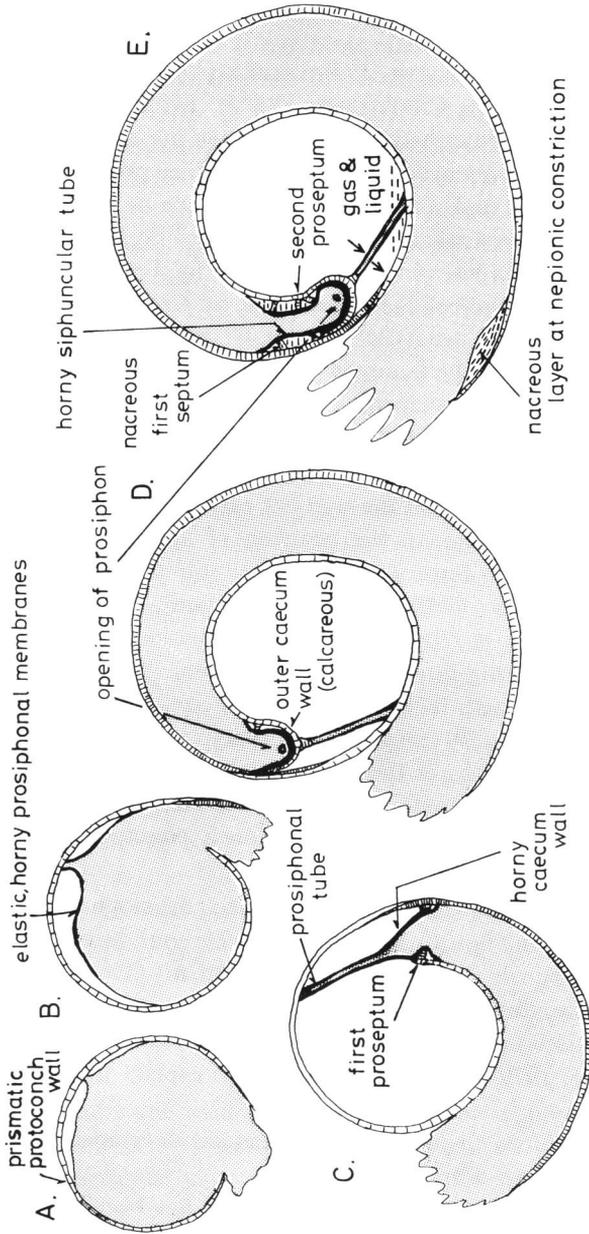
Fig. 4. Diagrammatic model showing the successive stages in the early ontogenetic development of the Ammonoidea based on the results of this work. A. 1st substage, B. 2nd substage, C. 3rd substage, D. 4th substage, E. transitional phase from the 5th substage (ammonitella stage) to the post-ammonitella stage. Ontogenetic development of internal shell structure at each substage is explained in the text. Soft tissues of a very young animal are shaded.

structure among the three taxonomically different groups (Ammonoidea, Spirulidae, Belemnoidea) is probably related to an identical configuration of the respective parts of the primary epithelium.

A part of the conclusion of BANDEL & BOLETZKY (1979) is, however, incorrect. As shown by GRANDJEAN (1910), CHRISTENSEN (1925), MÜLLER-STOLL (1936), and JELETZKY (1966), none of ever described belemnoids have the caecum and prosiphon in their phragmocone. The presence of an ammonite-like prosiphon and caecum have been confirmed in *Spirula* and some fossil coleoids such as the Cretaceous genus *Groenlandibelus* JELETZKY, 1966 (APPELLÖF, 1893, pl. 9, figs. 1–3; NAEF, 1922, figs. 9–11, 17, 21, 24, 27, 32–33; JELETZKY, 1966, pl. 21, fig. 1c, pl. 23, fig. 1c; BANDEL & BOLETZKY, *op. cit.*). The family Groenlandibelidae represented by *Groenlandibelus* and *Naefia* WETZEL, 1930 are placed in the order Sepiida by JELETZKY (*op. cit.*), but recently DONOVAN (1977, fig. 11) regarded the family as the ancestral group of modern *Spirula*. In modern *Nautilus* and *Sepia*, a cup-shaped caecum does not exist in the initial chamber (*see* STENZEL, 1964, fig. 66; BANDEL & BOLETZKY, 1979, fig. 14).

The above-mentioned similarity in the early internal shell structure between ammonoids and *Spirula* suggests us that the study of early ontogenetic development of *Spirula* will give an important clue to the problem of ammonoid early ontogeny. The embryonic development of *Spirula* is, however, still unknown. The smallest specimens described by CLARKE (1970) have a dorsal mantle length of about 2 mm. DENTON & GILPIN-BROWN (1971) reported another very young specimen (2.7 mm in mantle length) with a shell having three complete chambers. CHUN (1910) described mature ovarian eggs of *Spirula* with 1.7 mm in maximum size. Based on these reports, BANDEL & BOLETZKY (1979, fig. 19) have shown the hypothesis that *Spirula* hatches with the first chamber (protoconch) of the shell completed—possibly with the second chamber completed, if the mantle length of the newly hatched animal does not exceed 2 mm. They also have presumed that the protoconch contains some gas to give the animal neutral buoyancy at this stage.

The hypothetical model on the early ontogenetic development of *Spirula* of BANDEL & BOLETZKY (*op. cit.*, fig. 20) seems to resemble our model on ammonoid early ontogeny (*see* Fig. 4). In the model of ERBEN *et al.* (1969, figs. 4–5) on the ammonoid early ontogeny, the development of prosiphon and caecum was not fully described to our satisfaction. In this respect, the models of DRUSHCHITS *et al.* (1977b) and KULICKI (1974, 1975, 1979) are more reasonable to explain the ammonoid early ontogeny.

At present, we are inclined to judge that ammonoids developed directly without a larval stage like most modern dibranchiates.

Functional morphology of prosiphon and caecum: It has been generally accepted that all ammonoids may have had a planktonic mode of life at some early growth-stage (ERBEN, 1964, 1966; ERBEN *et al.*, 1969; DRUSHCHITS & KHIAMI, 1970; MATSU-MOTO, 1974; KENNEDY & COBBAN, 1976; DRUSHCHITS *et al.*, 1977b etc.). The floatation mechanism of a living ammonite at the early stage, however, has not yet been fully

demonstrated. We here discuss the functional implications of prosiphon and caecum in connection with the buoyancy problem.

As a result of this work, it has been made clear that in *D. semicostatus* and *E. haradai* the prosiphon is analogous to the siphuncle in the form and microstructure consisting of layered horny membranes; and, furthermore, that the inner layer of the caecum wall corresponds to the initial part of the succeeding siphuncular tube.

DENTON & GILPIN-BROWN (1966, 1971, 1973), DENTON *et al.* (1967), and COLLINS & MINTON (1967) have demonstrated that the siphuncular tube in the phragmocone of modern *Nautilus* and *Spirula* has an important function to control the buoyancy of living animals. Namely, the siphuncular tube wall in these animals is more or less permeable for fluids, and living animals can change the volume ratio of gas to liquid within camera with the successive pumping of liquid through the siphuncular wall. In another paper (OBATA *et al.*, *in prep.*) we are going to show that the microstructure and ultimate composition of siphuncular wall in several well-preserved late Cretaceous ammonite specimens from Hokkaido are closely similar to those of inner chitinous membranes in modern *Nautilus*. Based on this fact, we are going to conclude that the function of siphuncle in ammonoids for buoyancy control was essentially the same as that in *Nautilus*. That work may also give a light on the functional problem of ammonoid prosiphon and caecum. With respect to this problem, DRUSHCHITS *et al.* (1977b) presented an interesting hypothesis that the protoconch of a newly hatched post-embryonic ammonite was filled with gas and possibly, partly with liquid to maintain the planktonic mode of life. The results of this work may support their hypothesis. Furthermore, TANABE *et al.* (1979) showed that there is an intimate positive linear relationship between dimensions of protoconch and ammonitella among 28 late Cretaceous ammonites. This means a constant volume ratio of the air chamber (=protoconch) to the body chamber at the ammonitella stage.

In conclusion, at the early post-ammonitella stage the shell with prosiphon and caecum functioned as the buoyancy apparatus. The ammonite shell at this stage may have been partitioned into the protoconch filled with gas and some liquid, the second chamber septated by the second proseptum and first septum, and the subsequent body chamber (*see* Fig. 4-E), therefore, a young, probably early post-embryonic animal could control its buoyancy by controling the amount of liquid within the protoconch and the second chamber via the liquid-permeable prosiphonal and siphuncular walls.

Finally, we note the secondary function of prosiphon. CRICKMAY (1925) and SHIMIZU (1929) formerly suggested that the ammonoid prosiphon had a principal function as a transversal supporting "strut" to fix the position of caecum. Their assumption is indeed reasonable at least in part, but we furthermore consider that at the very early stage the organic membranes of prosiphonal tube were probably elastic and have such a subsidiary function as an elastic supporter during the gradual withdrawing of the soft body from the initial chamber (protoconch) (Fig. 4-A–C). The outer calcareous caecum wall apparently functioned as a septum to divide the

shell into the protoconch and the body chamber at the 4th substage shown in Fig. 4-D.

Concluding Remarks

The early ontogenetic development and functional morphology in the three late Cretaceous ammonites, *Mesopuzosia yubarensis*, *Damesites semicostatus*, and *Eupachydiscus haradai* have been studied in this paper by means of the SEM and EDX examinations on several well-preserved specimens from Hokkaido.

The internal structure of the ammonitella in these species is composed of protoconch, prosiphon, prosepta, caecum, septa, siphuncle, and shell wall with a nepionic constriction at the apertural end. The protoconch wall, outer caecum wall, shell wall in major part of the first whorl, and possibly prosepta are all formed of a prismatic or subprismatic calcareous layer, while the prosiphonal wall and inner caecum wall are made up of multi-layered membranes of horny material. The nacreous calcareous layer first appears in the first septum and the apertural area of the ammonitella; therefore, septa and the majority of siphuncle were secreted at the same time /or after the completion of the nepionic constriction. These observations are mostly agreeable with those of previous works on ammonoid early ontogeny. Based on the results obtained, we have proposed a hypothetical model of successive growth-stages in ammonoid early development (Fig. 4).

It has been well known that almost all modern dibranchiates develop directly without a larval stage. The early internal shell structure in ammonoids fairly resembles that in modern *Spirula* and some fossil coleoids in contrast to the great difference from modern and fossil nautiloids and *Sepia*. In the successive development of internal structure, our model well matches with those of Kulicki (1974, 1975, 1979) and Drushchits *et al.* (1977b) in which they stress the direct development of the Ammonoidea without post-hatching metamorphosis. It also closely resembles the hypothetical model of Bandel & Boletzky (1979) on the early development of *Spirula*.

The young, probably post-hatching ammonite at the stage after the completion of the nepionic constriction could control its buoyancy by controlling the amount of liquid within the gas-filled protoconch through the fluid-permeable horny membranes of prosiphonal tube wall, because there are morphologic and microstructural similarities between the prosiphonal and siphuncular tubes and because the volume ratio of air (protoconch) and body chambers at this stage is constant (*cf.* Tanabe *et al.*, 1979).

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Explanation of Plates

All photos by FUKUDA

Plate 1

Figs. 1–4. Scanning electron micrographs showing the early internal shell structure in the median section of three late Cretaceous ammonites. c: nepionic constriction. Acceleration voltage and scale (μ means μm) are shown at the base of each figure.

Fig. 1. *Damesites semicostatus* MATSUMOTO.　　GK. H 8085.　×70.
Fig. 2. *Damesites semicostatus* MATSUMOTO.　　GK. H 8039.　×70.
Fig. 3. *Eupachydiscus haradai* (JIMBO).　　GK. H 8024.　×100.
Fig. 4. *Mesopuzosia yuabrensis* (JIMBO).　　GK. H 8038.　×70.

Plate 2

Figs. 1–4. Scanning electron micrographs showing the microstructure of protoconch wall (1–2), septum (1), and ventral shell wall around the nepionic contriction (3–5) on GK. H 8024 of *Eupachydiscus haradai*. *See* Fig. 2 (in the text) for the position of each micrographs.

Fig. 1. Dorsal part of protoconch wall showing the subprismatic protoconch wall and the nacreous septum (s). ×1200.

Fig. 2. Part of protoconch wall near caecum, showing the inner prismatic (a) and outer subprismatic (b) layers. oc: outer calcareous layer of caecum wall. ×900.

Fig. 3a–b. Remarkable changes in ventral shell wall microstructure around the nepionic constriction. no: nacreous layer, p: prismatic layer of the first whorl, p′: prismatic layer of the second whorl, d: dorsal shell wall. Arrow indicates adoral direction. ×1200.

Figs. 4–5. Parts of ventral shell wall around the nepionic constriction, showing the microstructure of the inner nacreous (n) and outer prismatic (p) layers. c: tabular aragonite crystal, o: organic sheet, d: dorsal shell wall of the second-third whorls. ×4000 (Fig. 5), & ×4600 (Fig. 4).

Plate 3

Figs. 1–7. Scanning electron micrographs showing the internal microstructure of caecum wall and prosiphonal tube. μ under scale means μm.

Fig. 1. Internal microstructure near caecum. o & i: outer calcareous (o) and inner horny (i) layers of caecum wall. GK. H 8085 of *Damesites semicostatus*. ×400.

Fig. 2. Part of Fig. 1 showing the structural relationship between outer calcareous caecum wall

and prosiphon. ×1700.

Fig. 3. Part of Fig. 1 showing the multi-layered horny membranes of prosiphonal tube. ×4000.

Fig. 4. Outer surface of outer calcareous caecum wall. GK. H 8038 of *Mesopuzosia yubarensis*. ×1400.

Fig. 5. Structural relationship between outer calcareous caecum wall (oc) and prosiphonal tube. GK. H 8024 of *Eupachydiscus haradai*. ×1300.

Fig. 6. Part of Fig. 5 showing the multi-layered organic membranes of prosiphonal tube with a thin calcareous covering. ×4000.

Fig. 7. Part of outer calcareous caecum wall. GK. H 8024 of *E. haradai*. ×2100.

Plate 4

Figs. 1–6. Scanning electron micrographs showing the microstructure of inner horny caecum wall (1–2) and septal necks (3–6). Arrow indicates adoral direction. μ under scale means μm.

Figs. 1–2. Part of inner caecum wall showing the multi-layered organic membranes. GK. H 8039 of *Damesites semicostatus*. ×6500 (Fig. 1), & ×2500 (Fig. 2).

Fig. 3. Short prochoanitic septal neck at 2.5 π stage of GK. H 8039 of *D. semicostatus*. Organic siphuncular wall does not exist at the neck part. ×360.

Fig. 4. Long prochoanitic septal neck at 6 π stage of GK. H 8039. In this species septal necks tend to be longer with growth. ×85.

Fig. 5. Short prochoanitic septal neck at 3 π stage of GK. H 8024 of *Eupachydiscus haradai*. *See* the discontinuous siphuncular wall at the neck part. ×280.

Fig. 6. Short prochoanitic septal neck at 4 π stage of GK. H 8038 of *Mesopuzoisa yubarensis*. ×75.

Plate 5

Fig. 1. Scanning electron micrograph of a part of median-sectioned specimen, GK. H 8039 of *Damesites semicostatus*, showing the multi-layered organic siphuncular tube and nacreous septa. ×240 ($\mu = \mu$m).

Figs. 2–3. Characteristic X-ray images of silica (2) and calcium (3) on the same portion as Fig. 1. Same scales as Fig. 1. The shelly parts and organic siphuncular tube had been replaced by silica-rich material during diagenesis.

Fig. 4. Energy dispersive X-ray intensity spectra showing the semiquantitative ultimate composition on the same portion as Fig. 1.

Plate 2   TANABE, FUKUDA & OBATA: Ammonite Early Ontogeny

Plate 3

Plate 4   TANABE, FUKUDA & OBATA: Ammonite Early Ontogeny